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BLACKENING INDICES OF POTATOES GROWN UNDER VARIOUS CONDITIONS OF FIELD CULTURE[1]

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INTRODUCTION

In an earlier paper[2] the writers presented results from greenhouse cultures which indicated that the variety and relative instability of the seed stock are primary factors contributing to the darkening of boiled potatoes (*Solanum tuberosum*). The results described here were obtained with field plots on Antigo silt loam (Antigo, Wis.), Plainfield sandy loam (Hancock), and Miami silt loam (Madison). Hot, dry weather was characteristic of the summers during the early years of the study, and extensive areas produced tubers which blackened on cooking.

GENERAL PROCEDURE

Unless otherwise specified, certified seed stocks were used. Plots were 1 rod square on silt loam and 1 by 2 rods on the other soils. The fertilizer treatments were randomized by plots with replication on adjacent sections of the field. Application of the fertilizer (400 pounds per acre on sandy loams and 800 pounds on silt loams) was made by hand from a prepared portion of each plot. The fertilizer was placed in the hill, covered by soil, and the tuber was planted above it. Except limited trials of irrigation, the remaining care of the crop followed customary cultural practice.

A storage temperature for tubers of 60° F. was used prior to, and 40° F. during and after the 1939 trials. The experience of the writers indicates that the tendency to darken on cooking appears after about 2 months' storage at 40° F. and after about 1 month at 60°. The procedure for judging and expressing discoloration has been described.[3] Briefly, it consists of boiling 0.25-inch thick longitudinal slices from 10 tubers, cooling them by exposure to air, and comparing their discoloration with photographic standards. Tubers were scored as 0=white,

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[2] TOTTINGHAM, W. E., NAGY, R., ROSS, A. F., and others. A PRIMARY CAUSE OF DARKENING IN BOILED POTATOES AS REVEALED BY GREENHOUSE CULTURES. Jour. Agr. Res. 67: 177–193, illus. 1943.

[3] RIEMAN, G. H., TOTTINGHAM, W. E., and MCFARLANE, J. S. POTATO VARIETIES IN RELATION TO BLACKENING AFTER COOKING. Jour. Agr Res. 69: 21–31, illus. 1944. See also footnote 2.

1=light gray, 2=medium gray, and 3=dark gray. The scores for the 10 tubers were added and the sum divided by 0.3; thus if 10 tubers each scored 3 their sum of 30 divided by 0.3 would give the maximum blackening index of 100; a set of all medium gray tubers would have a blackening index of 66⅔, etc.

FIELD TRIALS

TESTS OF 1933

The test at Madison, Wis., in 1933 was designed to determine the effects of a liberal application of potassium to the soil and of irrigation on darkening of the cooked product. The complete fertilizer was a 2–10–12.5 mixture compounded from commercial sodium nitrate, 16 percent acid phosphate, and potassium sulfate. Four applications of water each lasting a half hour were made to each plot with a rotary lawn sprinkler. Canvas covers were applied to other plots to shed rain. The weather was very hot and dry in June (8.8° F. above and 2.1 inches below normal), hot in September (4.8° above normal), but otherwise essentially normal.

Tubers of the Irish Cobbler variety from plots which had been unfertilized or to which no potassium had been applied, cooked slightly gray after 2 weeks' storage, but all Rural New Yorker tubers boiled white. Longer storage might have changed the response somewhat.

TESTS OF 1934

The same plots were planted at Madison in 1934 as in 1933 but with a reversal of the controlled water relations. Other plantings[4] were made as follows: At Antigo; at Spooner in northwestern Wisconsin; at Almond near Hancock; at Tunnel City on sandy loam in western Wisconsin; and at Racine on Clyde silt loam in southwestern Wisconsin. A badly discoloring Rural New Yorker seed stock obtained from Tunnel City was used for comparison with a normal one. The fertilizer was similar to that used in 1933, but half the nitrogen was carried in cottonseed meal.

The weather record for Almond is taken from observations at Hancock and is so classed in figure 1. Spooner was wet in September (2.9 inches above normal) and dry in July (1.7 inches below normal). It was warm in June (3.0° F. above normal) and cold in September (3.4° below normal). At Tunnel City (Viroqua records) the precipitation alternated from wet to dry in successive months. This area was hot in early summer (8.6° and 5.0° above normal in June and July, respectively). Racine was wet in September (3 inches above normal) and dry earlier (average deficit of 1.6 inches in July and August). It was hot in June and July (5.0° and 2.6° above normal) and cool in September (2.7° below normal). These records together with those in figure 1 and table 1 show that the 1934 crop was subjected to heat at all locations during early vegetative activity but matured in cool weather. At Madison, Racine, and Spooner it was subject to drought until the generally heavy precipitation of September. This may have resulted in seriously reduced availability of mineral nutrients.

[4] The writers are indebted to Dr. J. C. Walker and Prof. J. G. Milward of the experiment station staff and to G. A. Johnson, a local producer, for care of the plots at Racine, Spooner, and Tunnel City, respectively.

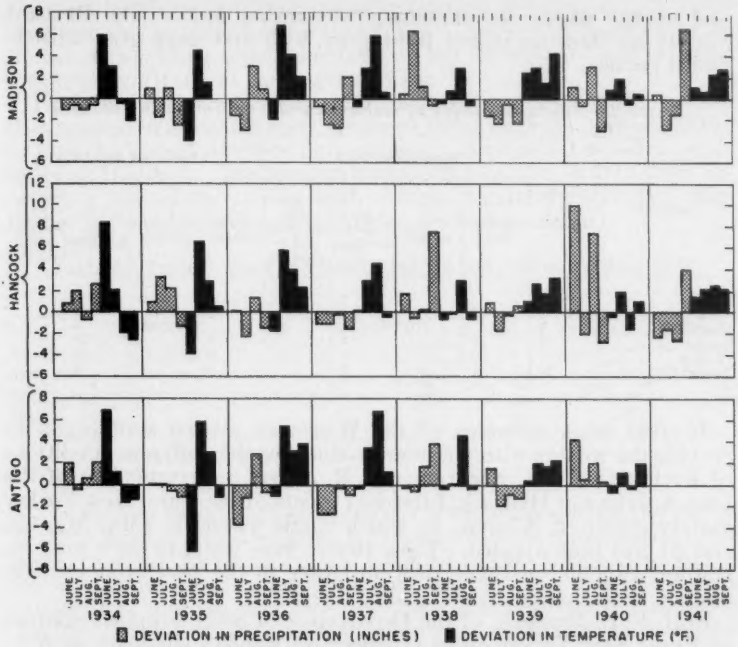

FIGURE 1.—Deviation in temperature (°F.) and precipitation (inches) from the normal mean values for the months of June, July, August, and September for the years 1934 to 1941, at the Madison, Hancock, and Antigo stations.

One-half of a sample of tubers taken at Almond about September 1 had peaked ends, while those from Antigo were mildly misshapen. The Almond crop from both seed stocks that received no potash cooked white. The crop from normal seed stock unfertilized at Antigo cooked light gray, and the crop from discoloring seed stock that received complete fertilizer became medium gray. Otherwise this crop cooked white regardless of fertilizer supply and irrigation. Immaturity of potatoes apparently is not a direct cause of blackening after cooking, for the immature tubers in this test showed no uniform blackening.

Boiling responses of the matured potatoes are shown in table 2. Blackening occurred independently of fertilizer treatment and irrigation and did not follow the discoloration response of the seed stock. With the exception of early heat the weather was relatively favorable,

TABLE 1.—*Normal mean temperature and precipitation values for the growing season of 1934 at the Madison, Hancock, and Antigo stations*

Station	June		July		August		September	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
Madison	67.2	3.76	71.8	3.88	70.0	3.21	60.0	3.72
Hancock	65.3	4.47	69.9	3.45	68.9	3.41	57.3	3.81
Antigo	63.0	4.38	66.6	4.1	65.7	3.23	56.3	4.03

and on the whole the darkening was rather mild. The Burbank variety at Madison scored light gray with and dark gray without added potash.

TABLE 2.—*Blackening index of mature Rural New Yorker tubers, 1934*

Location	Weeks after harvest	Normal seed stock				Discoloring seed stock			
		Unfertilized	No potash	Complete fertilizer	Complete fertilizer and irrigation	Unfertilized	No potash	Complete fertilizer	Complete fertilizer and irrigation
Almond	2		0	0			0	0	
Antigo	2	33		0		0		67	
Madison	2		0	33	33		33	0	33
Racine	3	67		0		0		33	
Spooner	3	0		0		0		33	
Tunnel City	20	0		0		0		0	

In 1934 other members of the Wisconsin station staff began to provide the writers with potatoes produced under different conditions of fertilization and irrigation. A. R. Albert, superintendent of the branch station at Hancock, furnished tubers of the Rural New Yorker variety grown at Almond, to which single materials (Mn, Mg, Ca, and S) had been applied. These tubers were white to dark gray on boiling without consistent relation either to the particular element applied or to changes in soil acidity.

Prof. F. L. Musbach, of the Department of Soils, supplied samples of Rural New Yorker crops produced on Kennan silt loam at Ashland in the extreme northern part of Wisconsin. Application of either manure alone (10 tons per acre) or manure (7.5 tons per acre) and 500 pounds of 3–10–6, 3–10–10, or 3–10–20 fertilizer led to white-cooking tubers throughout; the same results were obtained on Plainfield sandy loam at Spooner. Other tubers from Ashland produced on a second crop of clover supplemented by 800 pounds of 3–12–12 or 3–12–18 fertilizer showed slight bluish-gray discoloration on boiling. The weather at Ashland (Bayfield records) was only slightly cool and dry during the period from June to September (total deficit of 3.0 inches and monthly average of 1.3° F. below normal). However, August was distintly cool (3.3° below normal).

W. B. Ogden and Dr. James Johnson provided samples of Rural New Yorker potatoes produced on Miami silt loam at Madison. The plots had received lime and 10 tons of manure per acre before 3 successive years of cropping to tobacco. In the year preceding potatoes the crops had been legumes, timothy, tobacco, or a cereal grain. Eleven potato crops from such plots cooked white 3 weeks after harvesting.

TESTS OF 1935

The 1935 plots were located at Antigo (in another portion of the field planted in 1935 but still subject to previous overliming), at Arnott, and on both peat and loam at Madison. Examination of the surface soil sampled at planting[5] gave the results shown in table 3.

[5] For the soil analyses reported in this paper the writers are indebted to Dr. H. H. Hull of the Department of Soils of the University of Wisconsin.

The peat had been fertilized annually for corn production; a 3–11–16 fertilizer was applied for the potato test. Variations in practice included withholding either one-half of the nitrogen or one-third of the potash until tubers had begun to form.

The weather records show that precipitation was much greater than normal in July at Arnott (Stevens Point records), and continued so into the period of tuber development. September was dry, especially at Madison. The temperature at all locations shifted from excessively low to excessively high during vegatative activity. September was moderately cool at Antigo (Wausau records).

TABLE 3.—*Partial record of available nutrients in soils at planting, 1935*

Location	Phosphorus [1]	Potash [1]	Nitrate nitrogen [2]	pH
Antigo	90	175	20	6.1
Arnott	70	200	Trace	5.3
Madison, loam	125	350	33	6.0
Madison, peat	150	275	65	6.5

[1] Pounds per acre to a depth of 8 inches.
[2] Parts per million.

The boiling records given in table 4 were taken during the period from September 26 to December 1. Double columns represent replicate plots. Serious discoloration was confined to the Antigo crop and to susceptible varieties. Low potassium was at times associated with blackening; however, complete fertilizer did not prevent the trouble at Antigo. In general the results indicate some correlation of discolora-

TABLE 4.—*Blackening index of potatoes in relation to seed stock and fertilizer, 1935*

Location	Seed stock	Fertilizer application [1]				
		None	No potash	Complete	Late potash	Late nitrogen
Antigo	Burbank	33	67 67	67 0	0 0	0 0
	Cobbler	0	0 0	0 0	0 0	33 0
	Katahdin	0	33 0	0 0	0 0	0 0
	Rural New Yorker, normal	33	0 0	0 0	0 0	0 33
	Rural New Yorker, discoloring	0	33 33	67 0	0 0	0 0
Arnott	Burbank	0	33 0	0 0	0 0	0 0
	Cobbler	0	0 0	0 0	0 0	0 0
	Katahdin	0	0 0	0 0	0 0	0 0
	Rural New Yorker, normal	0	0 0	0 0	0 0	0 0
	Rural New Yorker, discoloring	0	33 33	0 0	0 33	0 0
Madison, on loam	Burbank	[2] 0	33	33	33	33
	Cobbler	[2] 0	0	0	0	33
	Katahdin	[2] 0	0	0	33	0
	Rural New Yorker, normal	[2] 0	0	0	0	0
	Rural New Yorker, discoloring	[2] 0	33	0	0	0
Madison, on peat	Burbank	------	0	0	------	------
	Cobbler	------	0	0	------	------
	Katahdin	------	0	0	------	------
	Rural New Yorker, normal	------	0	0	------	------
	Rural New Yorker, discoloring	------	0	0	------	------
Spooner	Burbank	0	------	0	------	------
	Cobbler	0	0	0	------	------
	Katahdin	33	33	0	------	------
	Rural New Yorker, normal	0	0	0	------	------
	Rural New Yorker, discoloring	0	0	0	------	------

[1] Double columns represent replicate plots.
[2] Complete fertilizer with irrigation.

tion with propensity of the seed stock and with fertilizer treatments. so into the period of tuber development. September was dry, especially at Madison. The temperature at all locations shifted from excessively low to excessively high during vegetative activity. September was moderately cool at Antigo (Wausau records).

Other samples produced under normal cultural conditions in northern Wisconsin were provided by Dr. J. C. Walker. Of these, the Chippewa, Cobbler, Katahdin, and Warba varieties were relatively white after boiling, whereas the Beauty of Hebron, Russet Burbank, and Rural New Yorker became appreciably gray.

TESTS OF 1936

In 1936 the field work at Antigo was transferred to another farm [6] in order to avoid soil conditions conducive to scab. In central Wisconsin the work was transferred to the branch agricultural experiment station at Hancock, where cultural operations were supervised by Prof. A. R. Albert. Other potato varieties were introduced and more extensive randomizing [7] of fertilizer treatment by plots and varieties in each plot was applied. Soil samples were taken at times of active assimilation of mineral nutrients by the crop.

The normal application of fertilizer on clay loam was 670 pounds per acre of 6–10–20, with nitrogen and potassium added as sulfates. Potassium was varied to half and double the normal amount, and on some plots the low potassium fertilizer was supplemented with farm manure (8.4 and 4.2 tons per acre on clay loam and sandy loam, respectively) or its equivalent of nitrogen as ammonium sulfate. In other cases the manure was supplemented by hydrated lime (1,670 pounds on loam, 835 pounds per acre on sand) or one-half its equivalent of nonalkaline "lime" as hydrated calcium chloride. Certain plots at Madison received the usual irrigation four times from July 7 to August 2.

Data for soil samples taken at planting were essentially the same as in table 3 (Hancock substituted for Arnott) except that values of 45 and 5 for phosphorus and nitrate at Antigo and 20 for phosphorus at Hancock should be substituted. Data covering available potash at harvesting appear in table 5. Availability remains better in the sandy loam than in the clay loams, suggesting potassium fixation in the clay loams during the dry season. The irrigated plots at Madison

TABLE 5.—*Soil content of available potash at harvesting in 1936*

Location	Unfertilized	No. K_2O	Low K_2O	Medium K_2O	High K_2O	Low K_2O with—		High K_2O with—	
						Manure	Ammonium sulfate	Lime hydrate	Lime chloride
Antigo	150	140	225	200	210	175	150	190	150
Hancock	125	175	200	225	340	260	140	225	250
Madison	275	275	.....	300	.....	.....	.....	[1] 325	[1] 325

[1] No K_2O.

[6] The writers are indebted to the owner, A. O. Reznichek, for constant interest in the project and faithful care of the crop.

[7] With the aid of Dr. J. H. Torrie, Department of Agronomy.

TABLE 6.—*Blackening index of potatoes produced in field plots at different locations, 1936*

Location and date of test	Variety	Fertilizer treatment								
		Unfertilized	No K_2O	Low K_2O	Medium K_2O	High K_2O	Medium K_2O +manure	Medium K_2O +$(NH_4)_2SO_4$	Medium K_2O +$Ca(OH)_2$	Medium K_2O +$CaCl_2$
Antigo; Oct. 23–24	Burbank	67	67	67	33	0	33	0	33	0
	Chippewa	0	0	0	0	0	0	0	0	0
	Cobbler	0	0	0	0	0	0	0	0	33
	Green Mountain	33	33	33	0	0	0	0	33	0
	Rural New Yorker	0	33	67	33	33	33	0	67	67
	Triumph	0	0	0	0	33	0	0	33	33
Hancock; Oct. 20–23	Burbank	33	67	33	0	67	67	33	0	33
	Chippewa	0	0	0	0	0	33	0	0	33
	Cobbler	0	0	33	33	33	0	0	0	0
	Rural New Yorker	67	67	67	33	67	33	67	67	67
	Triumph	0	33	0	0	0	0	0	0	0
						Irrigated				
				$(NH_4)_2SO_4$ only		No K_2O	Medium K_2O		$Ca(OH)_2$ only	$CaCl_2$ only
Madison; Nov. 1–3	Burbank		0	0	0	0	0	33	0	0
	Chippewa		0	0	0	0	0	0	0	0
	Cobbler		0	0	0	0	0	0	0	0
	Rural New Yorker		0	0	0	0	0	0	0	
	Triumph		0	0	0	0	0	33	0	0
						Manure only	Medium K_2O +B, Cu, Mn, Zn			
Spooner; Dec. 10	Burbank		33		33	33	33			
	Chippewa		0		0	0	0			
	Cobbler		33		33	33	33			
	Rural New Yorker		33		0	0	33			
	Triumph		0		0	0	0			

to which complete and potash-free fertilizer had been added were found to contain, respectively, 800 and 300 pounds of available potash per acre at harvesting.

At the Spooner branch experiment station duplicate plots were planted under the supervision of Professor Milward. A rare mineral mixture supplied 25 pounds of manganese salt, 10 pounds of copper salt, 5 pounds each of boron and zinc salts, and 1 pound each of salts of bromine, cobalt, iodine, molybdenum, selenium, titanium, and vanadium.

From figure 1 it is apparent that rainfall was seriously deficient during the main period of vegetative activity and became excessive in August. The temperature was more extreme, being much above normal after June. It seems probable that the prolonged heat was more conducive to blackening of the tubers than was the early drought.

The discoloration record is shown in table 6. Crops produced at Madison were characteristically free of blackening. In accord with their usual stability, the Chippewa and Triumph varieties were almost universally white on cooking, whereas the Burbank and Rural New Yorker discolored at all locations but Madison. The Cobbler was relatively free of blackening except in the Spooner crops; this may possibly be ascribed to difference in seed stocks. The Green Mountain produced at Antigo discolored mildly. The rarer elements did not prevent blackening of the crop at Spooner.

There is little correlation between the discoloration and omission of potassium from the fertilizer. Medium levels of potash appeared best, for the complete omission of fertilizer or more liberal applications of potash were more frequently followed by blackening. In the latter case it appears possible that higher concentrations of salts may have been injurious in a dry period.

After storage at 40° to 50° F. until the latter half of March the unfertilized and potash-deprived Burbank crops from Antigo and the Rural New Yorker crops from Madison cooked medium gray. In other cases these stocks had improved; the Antigo Rural New Yorker which had been supplied lime salts became white.

TESTS OF 1937

Primary attention was given in 1937 to potassium availability and to the application of rarer mineral elements. New soil areas were occupied at Antigo, Hancock, and Spooner. At Spooner each plot consisted of two rows 68 feet long following clover sod. The general fertilizer was a 3.5–9–18 mixture. Supplementary "x" and "y" salt mixtures were added as specified in table 7. The "x" mixture supplied per acre 6.2 pounds manganese, 2.5 pounds copper, 0.9 pound boron, and 1.1 pounds of zinc. The "y" mixture contained equal weights of salts of bromine, cobalt, iodine, molybdenum, selenium, titanium, and vanadium. Zinc was included in the "y" mixture applied at Antigo. Agrico carried rarer elements in unspecified forms and amounts. The application of ferrous sulfate carried 10 pounds of iron per acre. Examination of the soils from Antigo and Hancock before planting showed equal contents of available potash (155 pounds per acre) and ammonia nitrogen (35 pounds per acre) and similar acidity (pH 5.3 and 5.2, respectively). The available phosphorus and nitrate nitrogen

TABLE 7.—*Blackening index of potatoes in relation to seed stock and fertilizer, 1937*

Location	Fertilizer	Variety					
		Burbank	Chippewa	Cobbler	Green Mountain	Rural New Yorker	Triumph
Antigo	None	33	33	0	33	33	0
	No potash	33	33	33	33	33	67
	Low potash	0	0	0	33	33	0
	High potash	33	0	0	0	33	0
	Agrico	33	0	33	67	67	0
	Complete +B Cu	33	33	67	33	33	0
	Complete +B Mn	33	0	33	67	67	0
	Complete +B Cu Mn	0	0	0	67	67	0
	Complete +Cu Mn	0	0	0	33	67	0
	Complete +x+y [1]	67	0	33	0	33	0
	Complete +Fe	0	0	0	33	33	33
	Complete +Fe Cu	33	0	33	67	67	0
					Katahdin		White Gold
Hancock	None		0		33	67	67
	Complete	33		67	33	67	33
	Complete +x	67	0		33	67	33
	Complete +x+y	33	33	33	0	67	67
							Triumph
Madison	None	33	33	33		0	33
	No potash		0	0		0	33
	Irrigation, potash		33	67		33	33
	Complete		0	0		33	0
	Irrigation, potash			33		0	33
	Complete+x		0	0		67	33
	Complete +x+y		0	0		33	33
					Green Mountain		
Spooner	No potash		33	0	67	67	33
	Complete		33	33	67	33	0
	Complete +x+y		33	33	67	33	0
	Agrico		33	33	33	67	33

[1] For composition of x and y mixtures see p. 152.

of the Antigo soil (55 pounds per acre each) were about three and five times, respectively, the amount in the Hancock soil.

At the time of harvesting, samples of soil were taken at the four locations. These showed no consistent relations between available nutrients and fertilizer applications. The Antigo soil had become more alkaline (pH 5.5). The values were 5.4 for Spooner and 6.0 for Madison. Available phosphorus had increased in the Antigo soil to the same level as in the Madison soil (125 pounds per acre). At Hancock and Spooner it was double the original level at Hancock, or 50 pounds per acre. Available nitrogen was unchanged at Antigo but the ammoniacal form was four times that at Madison. Hancock had been depleted of available nitrogen to 5 pounds per acre of each form, but the similar soil at Spooner contained 40 pounds of nitrate and 15 pounds of ammonia nitrogen per acre. The data for potash were inconsistent in regard to increases with applications, but the average levels at Hancock and Spooner (about 170 pounds per acre) were little more than one-half those at the other locations. Samples of the subsoil taken at this time did not show a downward accumulation of available potash. It therefore seems probable that applied potash not assimilated by the crop was leached from the sandy soils and fixed by colloidal clay in the silt loams.

The Burbank stock was apparently a healthy one. It had been produced on peat soil at Coddington, Wis., in 1936 from stock grown in Idaho. The Cobbler stock was obtained from Prince Edward Island in 1935 and had been rogued at Antigo in 1936. The Rural New Yorker stock was provided by Professor Albert; the writers' plots were operated in conjunction with his at Hancock.

The principal boiling records are assembled in table 7. These display in the Antigo crops the notable records of the Chippewa and Triumph varieties for whiteness after boiling. The Green Mountain and Rural New Yorker varieties, and to a lesser extent the Burbank and Cobbler varieties, display their common susceptibility to blackening. Unfavorable regional effects are evident at Hancock with the Rural New Yorker variety and at Spooner with the Rural New Yorker and Green Mountain varieties. The 1936 tests at Madison with iron, boron, and copper supplements and with irrigation showed more serious darkening of the Chippewa and less darkening of the Triumph variety than in the 1937 tests. The Cobbler and Rural New Yorker varieties from Madison blackened frequently.

Extensive tests of single fertilizer constituents, and various levels and proportions of the major elements were conducted at Hancock in collaboration with Professor Albert. The Rural New Yorker used was light to medium gray after boiling; apparently the effects of heat and drought were dominant over the fertilization factors in the production of tuber pigment. However, it appears that high soil temperature alone was not the primary cause of the discoloration, for Dr. R. H. Larson repeatedly obtained relatively high records (over 90° F.) at a depth of 3 inches at Madison between mid-July and early September. Discoloration was not as serious in Madison, and corresponding soil temperatures did not induce blackening of greenhouse crops.

Professor Albert supplied samples from experiments dealing with the influence of different proportions of legume crop ploughed under and the application of farm manure. Tubers of the Katahdin variety produced on land from which only one crop of alfalfa had been removed in 1936 cooked light gray as compared with medium gray of a crop following alfalfa sod after two cuttings. This favorable effect of the larger crop residue was obtained from both unfertilized land and from land that had received 500 pounds per acre of 0–9–27. Rural New Yorker tubers from land manured after 6 years of cropping to alfalfa cooked light gray. These results seem to indicate a beneficial effect from maintaining the organic matter in the soil.

Other potato samples were supplied by Professor Musbach. The Green Mountain variety produced at Antigo under irrigation, either unfertilized or with the application of 600 and 2,400 pounds per acre each of 3–12–0 and 3–12–18, cooked white or light gray. Without irrigation, the crops produced without fertilizer and those produced by the use of 600 pounds of 3–12–0 cooked medium gray, but where 600 pounds of 3–12–18 was applied the discoloration was slight. The Rural New Yorker produced at Ashland by the addition of 7.5 tons per acre of manure or the same with 500 pounds of either 0–10–10 or 3–10–20 cooked light gray. So also did the crop on second growth of clover with 800 pounds per acre of 3–12–12.

Rural New Yorker tubers produced at Spooner after application of

7.5 tons of manure per acre cooked medium gray, but supplementary use of 500 pounds of commercial fertilizer containing different quantities of nitrogen and potash was followed by improvement to light gray. Land on which there had been second growth of clover plus 800 pounds of commercial fertilizer produced tubers which cooked light gray, even when the fertilizer contained 18 percent of potash.

Other samples, provided by J. L. Garrard, field agronomist of the American Potash Institute, were produced on peat at Coddington in central Wisconsin. Tubers of the Cobbler variety were essentially white after boiling, whether unfertilized or supplied 300 pounds per acre of nitrogen-free fertilizer. The fertilizer contained various combinations of phosphoric acid and potash, ranging from 0 to 20 and 0 to 50 respectively. The Rural New Yorker produced on Plainfield sandy loam with application of 300 pounds of 3–12–12 fertilizer and irrigation cooked medium gray. An unirrigated portion of the crop otherwise similarly treated remained acceptably white. Other samples became light gray, regardless of either omission or 50 percent increase of the potash supply and irrespective of 25 percent increase or decrease of phosphorus supply.

As figure 1 shows there was a marked deficiency of precipitation at Antigo during the vegetative period of June and July and a moderate deficiency during late tuberization in September. However, the most striking climatic departure was excessive heat during August. The high temperatures from July to September furnished a climatic hazard which might have induced the serious discoloration found at Antigo.

Hancock was subject to a mild deficiency of rainfall throughout the season. The weather was hot in July and especially in August. Although not as abnormal in this respect as at Antigo, the heat was probably more critical on the light sandy soil at Hancock. Tuber discoloration was most serious in the crop of this region.

Madison suffered severely from both heat and drought in July and August, and the crop showed practically as much discoloration as at Antigo.

Spooner, with a soil type essentially the same as that at Hancock, had a similar record of precipitation except a rainy July. Its temperature record was very similar to that of Hancock save for an excessively hot August. Except for Chippewa, the varieties grown at Spooner had the better boiling record, which might be expected from its cooler northern location.

Samples of potatoes produced by commercial growers near Antigo were made available to the writers. Cobbler and Rural New Yorker varieties were taken from fields of Felix Zeloski late in September. Immediately after harvesting, the Cobbler variety cooked white regardless of irrigation. The Rural New Yorker from an unirrigated portion of the field also cooked satisfactorily white, but the irrigated crop cooked light gray. The Rural New Yorker produced by L. D. Sargent with application of 3–9–16 fertilizer cooked fairly white where irrigated once, but light gray where irrigated four times. These results suggest that the effect of irrigation is to increase discoloration in boiled potatoes.

Different varieties of potatoes showed a distinct difference in blackening index when grown under the conditions of excessive heat and drought characteristic of 1937.

TESTS OF 1938

The planting at Antigo was on two of the replicate sections used in 1937. The "complete" fertilizer was a 3–10–18 mixture carrying nitrogen and potassium as sulfates. Elements of the x mixture were supplied in essentially the usual forms and amounts, with the exception of 10 pounds of boric acid per acre. Plots with straw mulch were added. The plots at Hancock were located on an area previously in general cropping. Three replications were made of the treatments shown in table 8. At Madison the plot tests were transferred to a sandy slope on the university campus. The higher and lighter soil of this area was devoted to a comparison of varieties, while the more clayey portion was used for application of various fertilizer combinations to the Rural New Yorker variety.

TABLE 8.—*Blackening index of potatoes in relation to variety and fertilizer, 1938*

Location	Fertilizer	Variety [1] [2]					
		Chippewa		Cobbler	Rural New Yorker		Triumph
Antigo	None	0	33	33	33	33	0
	No potash	0	0	33	33	33	0
	Low potash	33	33	33	33	33	0
	High potash	0	0	33	33	33	0
	Rarer elements	0	33	33	33	33	0
	Rarer elements −boron	0	0	33	33	33	0
	Complete +rarer elements	0	33	33	33	33	0
	Rarer elements −boron	0	0	33	33	33	0
	High potash, mulched	0	0	33	33	33	0
Hancock	None	0spr [2]	0	0spr	33spr	33spr	0
	No potash	0	0	0	33spr	33spr	0
	Low potash	0	0	0	33spr	67spr	0
	High potash	0spr		0	33spr	33spr	0
	Rarer elements	0spr	0	0spr	33spr	67spr	0
	Raror elements −boron	0spr	0	0spr	33spr	33spr	0
	Complete +rarer elements	0spr	0	0spr	33spr	33spr	0
	Complete −boron	0	0	0spr	33spr	67spr	0
Madison	Complete	0		0	33		0
	Complete +rarer elements	0		33	33		0

[1] Double columns represent replicate plots.
[2] Spr indicates occurrence of "spraing" or internal brown spotting.

At Hancock light "spraing" or internal brown spotting appeared to be of universal occurrence in the raw tubers of Rural New Yorker and of frequent occurrence in the Chippewa and Cobbler varieties. The evidence from the latter varieties indicates that spraing and blackening after boiling are not directly associated. Greenhouse cultures on sand had earlier shown a frequent occurrence of spraing when the moisture content of the sand was low. Freedom from blackening of the Cobbler crop at Hancock contrasts with its record of previous seasons, suggesting that the seed stock may have been unusually stable. The universal freedom of the Triumph variety from discoloration is characteristic of that variety.

Further cultural treatment of the Rural New Yorker at Hancock included the x mixture of rarer minerals (Mn, B, Cu, and Zn), together with molybdenum and cobalt, and the same without boron, applied both alone and in combination with a "complete" fertilizer. In some cases the K_2O was omitted from such mixtures. Tubers from all of these treatments cooked light gray, even when irrigated liberally.

During the vegetative period rainfall (fig. 1) was somewhat excessive at Hancock and Madison, and during September it was high at Hancock and Antigo. So far as temperature departures are concerned, the only serious abnormalities seem to be the high temperatures in August.

Cobbler and Chippewa tubers produced at Antigo blackened after boiling; those produced at Hancock cooked normally. Discoloration of the Chippewa variety is rare. The Triumph retained its record for whiteness of cooking at all three locations. Inherited varietal differences appear to be a major factor in tuber discoloration.[8]

Samples of Rural New Yorker tubers produced at Ashland on Superior clay loam were supplied by Professor Musbach. The tubers produced on the lower levels of potash with manure (no fertilizer or 3–10–6) and those following clover cooked medium gray. Those following manure supplemented by higher levels of potash cooked light gray and darkened only mildly at the stem ends. The Rural New Yorker was also produced on Plainfield sandy loam at Spooner. Only the lower levels of potash (no fertilizer and 3–10–6) were associated with medium grayness of the cooked tubers, all of the others becoming light gray. The Triumph variety was also produced at Spooner; borax was added alone (10 pounds) and at different levels (5, 10, 20 pounds) in combination with 600 pounds of 3–12–12 fertilizer. The crops that were supplied the low borax mixture, both irrigated and unirrigated, and those supplied the borax-free mixtures unirrigated, cooked light gray while all the others remained white. This would seem to show a correlation between discoloration and boron deficiency, but such an interpretation is not supported by the total experience of the writers.

The major climatic abnormality at both Ashland and Spooner was excessive heat in August. In addition, the latter location suffered a deficiency of rainfall until August. It appears probable that of the climatic factors that might have influenced the results, heat was primarily responsible for inducing darkening of the susceptible Rural New Yorker variety in both locations.

TESTS OF 1939

The primary object of the 1939 test was to determine the effect on discoloration of tubers of different levels of boron supplied in conjunction with different levels of potassium in a "complete" fertilizer. A highly purified muriate of potash (KCl) low in boron was used. Phosphorus was supplied in calcium metaphosphate (61 percent available P_2O_5) and nitrogen as ammonium sulfate. Five, 10, or 30 pounds of borax were added to an 800-pound-per-acre quantity of "complete" fertilizer. Also, 40 pounds of borax was applied as a supplement with 25 pounds of manganese salt. As a more complete treatment this formula was supplemented by 5 pounds each of copper and zinc salts together with 1 pound each of salts of cobalt, iodine, molybdenum, selenium, thallium, titanium, and vanadium. At Hancock, on sandy soil, fertilizers were applied at one-half of these rates. These plots were relocated on new areas at Antigo and Hancock but not at Madison. In the Madison area the rate of application of fertilizer was increased to 1,200 pounds per acre.

[8] See footnote 3, p. 145.

A partial record of the composition of these soils in the midst of cropping is shown in table 9. At Antigo a liberal supply of potassium was followed by a sustained abundance of this element in the soil, but the results at Hancock were somewhat erratic. There was a notable increase of nitrate with increase of potassium supply at both Antigo and Hancock.

TABLE 9.—*Partial composition of soils in early August 1939*

Location	Available P	Available K_2O	N as NO_3	N as NH_3	pH
Antigo:					
Low K	80	160	20	40	5.5
Medium K	60	170	25	45	5.2
High K+high B	95	280	35	40	5.3
Hancock:					
Low K	105	180	25	30	5.2
Medium K	80	170	35	25	5.0
High K	65	260	40	25	4.9
High K+low B	60	160	50	30	5.0
Madison:					
Sandy area, east	200	400	60	40	7.0
Sandy area, west	160	400	75	45	6.3
Loamy area, east	100	200	50	35	7.0
Loamy area, west	220	450	75	40	6.3

The plots at Madison were deficient in rainfall in both June and July; the other stations were deficient in July only. In August and September rainfall was deficient at both Antigo and Madison. This was a season of prolonged but mild heat in which Antigo, Hancock, and Madison suffered increasingly in the order named.

Records of the color of the potatoes after boiling are assembled in table 10. These are general averages, largely of 2 samples from different plots at Madison and of 3 samples from the other locations. The total record of the Chippewa variety was 9 light gray and 30 white samples at Antigo, 5 slight to light gray and 30 white at Hancock. Thus, the discoloration after cooking was at least no greater in the sandy area at Hancock than farther north. It is worthy of note that most of the cases of spraing occurred independently of darkening after boiling.

TABLE 10.—*Blackening index of potatoes produced in field plots, 1939*

Location and date of test	Treatment	Chippewa	Cobbler	Rural New Yorker; normal	Rural New Yorker; discoloring A	Rural New Yorker; Discoloring B
Antigo: (Boiled Nov. 27–Dec. 5; average of 3 plots.)	Low K	11	33	33	22	22
	Low K+low B	0	22	33	33	44
	Low K+medium B	0	33	33	22	33
	Low K+high B	16	44	33	22	44
	Medium K	11	44	33	22	22
	Medium K+low B	0	22	11	22	33
	Medium K+medium B	33	44	22	11	33
	Medium K+high B	0	33	22	44	33
	High K	11	44	33	11	22
	High K+low B	0	33	22	16	22
	High K+medium B	0	33	22	22	44
	High K+high B	11	33	22	33	44
	High K+high B+Mn	22	44	33	22	33
	High K+high B+x+y [1]	0	33	22	22	33

[1] For composition of x and y mixtures see p. 152.

TABLE 10.—*Blackening index of potatoes produced in field plots, 1939*—Continued

Location and date of test	Treatment	Chippewa	Cobbler	Rural New Yorker; normal	Rural New Yorker; discoloring A	Rural New Yorker; Discoloring B
Hancock: (Boiled Dec. 7–13; average of 3 plots.)	Low K	0	50	0	------	33
	Low K+low B	0	22	22	33	0
	Low K+medium B	0	22	11	0	0
	Low K+high B	11	11	22	0	11
	Medium K	0	22	33	0	33
	Medium K+lowB	0	0	33	0	33
	Medium K+medium B	0	0	33	33	33
	Medium K+high B	11	11	16	0	33
	High K	0	0	33	0	22
	High K+low B	0	22	33	0	33
	High K+medium B	0	22	11	------	50
	High K+high B	0	22	16	16	0
	High K+B+Mn	11	11	11	------	------
	High K+high B+x+y	0	22	44	0	------
Madison: (Boiled Nov. 13–14; Rural New Yorker section; average of 2 plots.)	Complete	0	16	0	------	0
	Complete+x	0	0	0	------	0
	Unfertilized	------	------	0	------	------
	x only	------	------	0	------	------
	x+Co, Mo	------	------	0	------	------
	x+B	------	------	0	------	------
	Complete high K	------	------	0	------	------
	Complete High K+x	------	------	16	------	------
	Complete low K	------	------	0	------	------
	Complete low K+x	------	------	0	------	------

The Cobbler produced at Antigo included 8 samples that boiled medium gray, 27 light gray, and only 3 that showed no discoloration. This record was much worse than that at Hancock, which included 17 light-gray samples, 19 white, and 15 cases of light spraing. Of 3 stocks of Rural New Yorker planted at Antigo and Hancock, 2 produced tubers that turned light gray after boiling. These formed the source of the discoloring seed stocks A and B shown in table 9. From the progeny of normal Rural New Yorker stock there were 34 samples that boiled slight to light gray and 8 that boiled white at Antigo; at Hancock there were 1 medium gray, 20 light gray, and 10 white. Discoloring Rural New Yorker seed stock A yielded 26 light-gray samples and 10 white ones at Antigo, as compared with 13 white and 3 light-gray at Hancock. Discoloring Rural New Yorker seed stock B produced 3 medium-gray samples, 36 light gray, and 4 white at Antigo, as compared with 2 medium gray, 21 light gray, and 4 white at Hancock. The general record of discoloration was more serious throughout in the Antigo crop; spraing and dark stem ends were confined to the Hancock crop. As usual, the Madison crop was notable for its whiteness without regard to the seed stock planted. The weather records indicate that the season was somewhat hot and dry but not excessively so and the weather abnormalities were about the same at the three stations (fig. 1). On the whole, there was no great difference in the response of the normal and discoloring Rural New Yorker seed stocks at Antigo; the discoloring stock A gave the best results at Hancock. No correlation was found between boron supplied and the degree of darkening after cooking.

TESTS OF 1940

The plantings at Antigo and Hancock were on land not recently used for potatoes. Six plots were treated with a low potassium fertilizer (6–12–6) and six with a high potassium fertilizer (6–12–18). Ten seed stocks were planted, the order being randomized for each pair of adjacent low and high potash plots. This arrangement gave a triplicate test of each fertilizer formula. Five of the stocks had cooked acceptably white and five had turned appreciably dark. The stocks used were predominantly from the Rural New Yorker variety.

Antigo and Hancock had a considerable excess of rainfall during both the early vegetative and the early tuberizing periods of the crop. Except for possible early removal of nutrients from the soil at Antigo, these departures seem likely to have favored rather than interfered with the plants. At Hancock, however, the great excess of precipitation during these periods must surely have led to serious depletion of fertility in the sandy soil. The departures of temperature from normal were probably too small to cause any disturbance in plant development.

The results from a determination of available mineral nutrients in soil samples taken the first week in October appear in table 11. These show an accumulation of potassium in all cases following the higher application of potassium. A native deficiency of phosphorus in the sandy soil at Hancock seems to have been substantially offset by the fertilizer application. The usual predominance of nitrate over the ammoniacal form of nitrogen is here largely reversed in the Miami silt loam. Dr. K. C. Berger, of the Department of Soils, who determined available boron in soils from areas planted at Antigo, Hancock, and Madison from 1937 to 1939, found overlapping values at the different locations in the range 0.2–0.5 p. p. m., so that it does not appear that deficiency of this element is associated with the tuber discoloration in question.

TABLE 11.—*Available nutrients in soil at the close of the cropping season, 1940*

Location	Available P	Available K_2O	N as NO_3	N as NH_3	pH
Antigo:					
Unfertilized divider rows	100	145	Trace	20	5.2
Composite low-K plots	100	150	Trace	20	4.8
Composite high-K plots	85	210	5	20	4.8
Hancock:					
Unfertilized divider rows	30	140	Trace	20	5.0
Composite low-K plots	50	150	Trace	15	4.9
Composite high-K plots	110	220	15	20	4.9
Madison:					
East (sandier) side of plots	110	310	40	10	6.4
West (more loamy) side of plots	110	440	30	5	6.4

The boiling records of the crops described above are shown in table 12 as the average of three plots per seed stock, except for single plots at Madison. Discoloration was erratic. Seed stock No. 5 was Triumph, No. 7 was Cobbler, and the others were of the Rural New Yorker variety. Although the normal seed stocks showed a better record than discoloring seed stocks on low potassium fertilization, this was not true on high potassium. Tubers from the discoloring seed stocks were not appreciably inferior, despite the fact that this group had a Cobbler (No. 7) to balance the white-cooking Triumph (No. 5) of the normal group. The more liberal supply of potassium seems to

TABLE 12.—*Blackening index of potatoes*[1] *produced in field plots, 1940*

Location	K level of fertilizer	Normal seed stocks					Discoloring seed stocks				
		1	2	3	4	5	6	7	8	9	10
Antigo	Low K	33	22	33	44	0	33	33	56	33	33
	High K	33	22	11	11	0	0	33	11	11	11
Hancock	Low K	22	11	22	22	0	44	22	33	33	22
	High K	33	44	33	33	11	33	0	22	22	33
Madison	High K	0	0	0	0	------	0	------	0	0	0

[1] Seed stock No. 5 was the Triumph variety, No. 7 was Cobbler, and the rest were Rural New Yorker

TESTS OF 1941

be associated with the production of more normal tubers, except at Hancock, with normal seed stocks.

Because of the negative results in previous years of attempts to control blackening after boiling by the application of fertilizer, plot operations were restricted in 1941. At Hancock two plots were treated with 3–10–12 fertilizer supplemented by the x mixture of minor elements, and a third plot was treated with the same fertilizer except that the percentage of nitrogen was doubled. The potassium chloride salt was low in boron.

At Madison, on the sandy area, one section was unfertilized and another was treated with the fertilizer supplemented by minor elements, as applied at Hancock. In addition to the certified stocks planted here, stocks which discolored after cooking but appeared otherwise normal were separated into tubers normal and abnormal on the basis of cooking tests with individual tuber sections ("indexed" tubers, table 13). These were planted in separate sections of a row fertilized as described above.

Other plantings were made on Miami silt loam at the university farm adjacent to the campus. These were on small plots (0.0055 acre) which received low, medium, and high applications of KCl (125, 250, and 500 pounds per acre respectively), with unfertilized check plots. Relatively high levels of calcium hydroxide and calcium sulfate (gypsum) at the rate of 1,000 pounds each per acre, were applied both without and with potassium in proportions indicated with the data. The rows were placed 6 feet apart, with a distance of 2 feet between hills.

Hancock suffered from a considerable deficiency of rainfall except during tuberization of late varieties (fig. 1). Madison had an equal

TABLE 13.—*Blackening index of potatoes produced in field plots, 1941*

Location and treatment	Chippewa	Cobbler	Rural New Yorker	Indexed Chippewa		Indexed Rural New Yorker	
				White	Gray	White	Gray
Hancock:							
Unfertilized	0	0	33	------	------	------	------
Normal fertilizer	0	0	33	0	33	33	66
High-N fertilizer	0	0	33	0	0	33	33
Low-N fertilizer	0	0	33	------	------	------	------
Madison:							
Unfertilized	0	0	0	------	------	------	------
Normal fertilizer	0	0	0	0	0	------	------

deficit during the period July-August, but the type of soil at this location was more tolerant of drought. At both locations the crop was subjected to temperatures considerably above normal.

The boiling records are assembled in table 13. As usual, the crops at Madison were notably free from discoloration. At Hancock the Rural New Yorker variety was distinguished from the other varieties by its susceptibility to blackening. The comparison of normal with discoloring seed stocks shows some indication of a carry-over of this response to the succeeding crop.

RESULTS WITH SELECTED SEED STOCKS

For the plantings of 1939 seed stocks of Rural New Yorker and a few other varieties were obtained from a number of growers in Wisconsin. In addition, stocks of different varieties were obtained from potato specialists in other States. The object of this phase of the work was to determine whether the cooking response of the crop was maintained under different climatic and soil environments. Uniform fertilizer and cultural treatments were applied throughout for these crops on portions of the field plots at Antigo, Hancock, and Madison.

The records of crops produced from these stocks in 1939 are shown in table 14. The tubers produced at Hancock discolored somewhat more than those from Antigo. The tubers from Madison cooked white.

TABLE 14.—*Blackening index of crops produced from selected seed stocks at different locations, 1939*

Source of seed stock	Variety and stock	Boiling record of seed stock	Boiling record of crop at—		
			Antigo	Hancock	Madison
Colorado:					
A	Rural New Yorker	0	33	67	
B	Burbank	67	0	67	
B	Rural New Yorker	67	33	67	0
Idaho:					
A	British Queen	33	33	33	
A	Burbank	33	33	0	
A	Idaho Russet	33	0	33	
Maine:					
A	Rural New Yorker	0	33	33	0
B	Chippewa	0	0		
B	Cobbler	33	0		
B	Rural New Yorker	33	0		
Minnesota: B	Red Warba	0	0	0	
Nebraska:					
A	Chippewa	0	0	0	
A	Cobbler	0	67	33	
A	Triumph	0	0		
B	Chippewa	0	0		
B	Cobbler	0	33		
B	Triumph	0	0		
New York: A	Rural New Yorker	67	33	33	0
Wisconsin:					
A	Early Ohio	0	0		
A	Early Rose	0	0	33	0
A	Red McClure	0	33	67	
A	Discoloring (indexed Rural New Yorker).	67	67	67	
B	Sprained (selected Rural New Yorker).	0	33	33	0
A	Sebago	0			0
C	Rural New Yorker	33	0	67	0
D	do	33	33	33	0
A	Triumph	0	0	0	0
E	Rural New Yorker	0	0	67	
F	do	0	33	33	

The response of the crop was not consistently related to the boiling record of the stock. Six of the 28 stocks planted at Antigo produced crops showing increased discoloration and 7 stocks showed the reverse relation. Eight of 20 stocks planted at Hancock produced crops showing increased discoloration and only 2 produced less discoloring crops. Thus about 50 percent of the stocks at each station showed no change. At Antigo the effect of the change of environment was indefinite and at Hancock it was unfavorable to whiteness of the cooked crop. The few stocks tested at Madison showed a favorable effect of location upon the boiled tubers.

The crops produced from these seed stocks at Antigo in 1939 were used as planting stock for a repetition of the test in 1940. Results of the boiling tests are assembled in table 15.

TABLE 15.—*Blackening index of crops produced from selected seed stocks at different locations, 1940*

Source of seed stock	Variety	Boiling record of seed stock	Boiling record of crop at—		
			Antigo	Hancock	Madison
Colorado:					
A	Rural New Yorker	0	0		0
B_1	Burbank	67	0	0	0
B_2	Rural New Yorker	67	0		0
Maine:					
A	Rural New Yorker	0	0	33	0
B_1	Cobbler	0			0
B_2	Green Mountain				0
B_3	Rural New Yorker	67	0	0	
Minnesota	Red Warba	0	0	0	0
Nebraska:					
A_1	Cobbler	0	0	33	
A_2	Triumph	0	0	0	
B_1	Cobbler	0			0
B_2	Triumph	0	0	0	
B_3	Chippewa	0			0
New York	Rural New Yorker	67	0	67	0
Wisconsin:					
A_1	do	33		67	0
B_7	do	33	33	33	0
D_{10}	do	0	0	33	
E_{26}	do	0	0		
Antigo	Triumph	0	0	0	0
Hancock	Rural New Yorker	0	0		
	Cobbler	0	0	0	
	Triumph	0	0	0	
Madison	Rural New Yorker	0	0	0	
	Chippewa	0	0	0	0

None of the crops produced at Antigo showed greater discoloration than the original seed stock. Five showed less discoloration. About 80 percent showed no change. Approximately one-half of the crop produced at Hancock discolored no more than the original stock, about one-sixth discolored less, and one-third discolored more. Conditions at Hancock again induced discoloration of unstable varieties. All of the 14 stocks tested at Madison cooked white, which is in accord with the results of the test in 1939. The 1940 season was less conducive to discoloration than that of 1939 (fig. 1).

DISCUSSION AND SUMMARY

The tests reported here covering field trials over a period of 9 years, were designed to ascertain the influence of climatic and cultural conditions and potato varieties on the blackening of potatoes after boiling. By extending the trials over a number of years at several stations a variety of soil types and climatic conditions were encountered, and it

was possible to test numerous potato varieties and strains and to employ a number of different fertilizer treatments.

These extensive tests show no single factor or combination of factors to be uniformly responsible for blackening of potatoes on boiling; rather, they emphasize the complexity of the factors governing this response of tubers.

Diverse fertilizer treatments on different soils, including the use of both the macro- and micro-nutrient elements, gave little consistent alleviation of blackening in the tubers grown. The only fertilizer element that exerted any marked control of blackening was potassium. Frequently a high level of potassium decreased blackening noticeably, but this response was not uniform even within an experiment. To attribute any specific action to potassium or any other nutrient element in controlling blackening is unjustified by data thus far accumulated.

That climatic or soil conditions are involved in blackening was strongly suggested by the fact that potatoes grown at Madison consistently boiled whiter than those produced at other locations. In the absence of substantial evidence that mineral nutrition governs blackening of tubers, climatic factors are implicated. Judging by the yearly incidence of blackening in market potatoes, one would conclude that the trouble was associated with growth in a hot, dry season. However, the hottest and driest station among those reported is Madison, and there the least blackening occurred. In contrast to the general observation that hot, dry seasons induce a tendency to blacken, Smith, Nash, and Dittman [9] found that little or no blackening occurred in potatoes which matured when the mean temperatures were 70° F. or higher, but potatoes which matured when the mean temperatures were 60° or lower often blackened. Blackening could be prevented by exposing susceptible tubers to 100° for 3 to 4 days. Consistent with the view of Smith et al., Madison had the highest mean temperature during the maturation period and the lowest incidence of blackening. Climatic factors evidently influence the tendency to blacken, but the data are not sufficiently consistent to permit a precise definition of the conditions that cause it.

Variety more directly than any other factor governs the blackening of potatoes.[10] It is rare that Chippewa, Triumph, or Sebago potatoes cook black regardless of the conditions under which they are produced; in contrast, Rural New Yorker, Irish Cobbler, and some other varieties often cook black.

Fertilization with the macro- and micro-nutrient elements does not insure the production of potatoes that will remain white on boiling, and approach to the problem from this direction currently holds little promise. Climatic conditions evidently are involved, but the governing factors are ill-defined, and aside from control of water supply by irrigation they cannot be altered appreciably. On the other hand, a rather consistent blackening or nonblackening response is predictable on the basis of tuber varieties. In the present state of our knowledge, probably the best assurance of producing nonblackening potatoes rests in the selection of proper varieties, e. g., Triumph, Chippewa, and Sebago, which regularly yield acceptable tubers.

[9] SMITH, O., NASH, L. B., and DITTMAN, A. L. POTATO QUALITY VI. RELATION OF TEMPERATURE AND OTHER FACTORS TO BLACKENING OF BOILED POTATOES.—Amer. Potato Jour. 19: 229–254. 1942.

[10] See footnote 3, p. 145.

PREDISPOSITION OF TOMATO TO FUSARIUM WILT[1]

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INTRODUCTION

Fusarium wilt (*Fusarium oxysporum* f. *lycopersici* (Sacc.) S. & H.) of tomato (*Lycopersicon esculentum* Mill.) is a representative of the vascular fusarial diseases. In this group of maladies, the pathogen, after gaining entrance into the plant through the root system, becomes established in the xylem where toxic materials are produced which pass throughout the plant, bringing about yellowing and wilting of the leaves and stem and later causing death. Two rather distinct phases of host development enter into the complex which determines its susceptibility or resistance to the pathogen. One of these is the effect of the xylem contents on growth of the pathogen and the production of toxic materials. The other is the anatomical and physiological make-up of the plant which determines the degree to which it resists or succumbs to the pathogen.

Observations made during the course of previous studies (*24*)[3] led the authors to believe that wilt development may be affected not only by environal factors existing during infection and disease development, in which case the first phase mentioned above is primarily concerned, but also by factors acting upon the plants before infection and in some manner altering their susceptibility or resistance, in which case the second phase may be expected to be the one involved. It was indicated that control of environal factors acting upon the host alone for a period of time before infection might bring about differences in subsequent disease development distinct from the influence of such factors acting upon the host-pathogen complex after infection. The concept is one which has received little study in the general field of the relation of environment to disease development.

Previous studies have nearly always included the effect on disease development of factors in the environment acting before, during, and after infection of the host. It is, therefore, difficult to determine to what extent those factors were effective in predisposing the host to infection and disease development. Dickson (*6*) found in the case of seedling blights of corn and wheat (*Gibberella saubinetii* (Mont.) Sacc.) that soil temperatures influenced the susceptibility of the

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[2] The writers wish to express their appreciation to Mr. Eugene Herrling for preparation of the illustrations.

[3] Italic numbers in parentheses refer to Literature Cited, p. 184.

hosts to disease. Wheat seedlings were more severely infected when grown at high soil temperatures, while corn seedlings succumbed more rapidly when grown at low soil temperatures. Dickson and Holbert (*8*) showed that marked changes in the metabolism of corn seedlings occurred at the same temperature at which susceptibility to blight was increased. Shaw (*19*) found that both soil and air temperatures before infection affected the susceptibility of apple shoots to fire blight (*Erwinia amylovora* (Burr.) Bergey et al.). A number of workers (*7*, *18*, *19*, *23*) have noted that the water content of the soil affected the host in such a way as to render it more or less susceptible to disease. The effect of nutrition on the development of host-parasite relations has received considerable attention, but only limited studies on the relation between host nutrition and predisposition to disease have been reported (*5*, *11*, *13*, *18*, *19*, *22*). That a given plant may be more susceptible to disease at one stage of development than at another is a well recognized fact. According to Blank (*2*), older cotton seedlings showed a greater susceptibility to *Phymatotrichum omnivorum* (Shear) Dugg. that did very young seedlings. Shaw (*19*) observed that apple shoots decreased in susceptibility to fire blight with age. Anderson (*1*) found no differences in susceptibility to yellows (*Fusarium oxysporum* f. *conglutinans* (Wr.) S. & H.) in cabbage plants of different ages. In certain cases, greater disease development has been observed on the more vigorously growing host plants, as pointed out by Piemisel (*14*), Kyle (*12*), Raines (*16*, *17*), and Shaw (*19*). Pritchard and Porte (*15*) stated that favorable conditions for growth of tomato plants increased their susceptibility to leaf spot (*Septoria lycopersici* Speg.). In direct contrast to the foregoing, Dickson, Eckerson, and Link (*7*) found that low vegetative vigor predisposed corn and wheat seedlings to infection by *Gibberella saubinetii*.

The purpose of this investigation was to determine in what way and to what extent certain factors in the environment may bring about predisposition to fusarium wilt in tomato plants. By studying the effects of variations in the environment given the host plant only before infection, an attempt was made to determine the effect of environment on disease development through its action upon the host alone and to eliminate as much as possible the effects of environment on the disease complex. This was accomplished by varying a given factor in the environment in which healthy young tomato plants were grown for a period before inoculation, and studying the development of disease after infection when the plants were growing under uniform conditions for wilt development.

The term "predisposition," as employed in this paper, refers to any modification of the host plant brought about by environal or nutritional factors previous to infection which influences the expression of the disease symptoms after infection. An attempt was made in this investigation to distinguish such effects from those of environment and nutrition after infection and from those of inherent degrees of resistance or susceptibility characteristic of certain strains of the host plant.

MATERIALS AND METHODS

In all experiments, three types of hosts were used. Bonny Best (*Lycopersicon esculentum* Mill.) represented the class very susceptible

to wilt; Marglobe (*L. esculentum*), which has been used commercially with a fair degree of success in many wilt-infested areas, represented the class of varieties which have an intermediate degree of resistance; a strain of Red Currant tomato (*L. pimpinellifolium* Mill.) represented those strains or varieties highly resistant to wilt, in which resistance is inherited as a qualitative character and controlled by a single gene (*3*).

These hosts were sown in soil free from the wilt organism or in washed sterilized fine white silica sand, and were transplanted approximately 3 weeks later when the first true leaves were forming. The plants were grown for a period of from 30 to 50 days under environal conditions which were near the optimum for vigorous growth except for the single predisposing factor being varied. Predisposing conditions will be described for each series of experiments under Experimental Results. All other conditions not under test were kept as uniform as possible. At the end of the predisposing period, all plants were inoculated with a virulent strain of the organism according to the method outlined by Walker and Foster (*24*). After inoculation, the plants were all given the same environal conditions, which were maintained as near as possible to the optimum for the development of wilt, unless otherwise indicated. Disease indices were calculated (*24*) for each type of host grown under each predisposing condition. At least 20 plants of each host type were given each variation in environment in each experiment, and 2 or more experiments were conducted for each predisposing condition under test.

EXPERIMENTAL RESULTS

PREDISPOSITION BY SOIL TEMPERATURE

Ten plants of each host type were grown in clean compost soil in each of 8 crocks in a Wisconsin soil temperature tank. Soil in the crocks was insulated from the air by a 1-inch layer of ground cork and the moisture content was maintained at the optimum by adding enough water daily to bring the crocks up to original weight plus estimated plant weight. Tanks were adjusted to maintain soil temperatures of 12°, 20°, 28°, and 36° C., while a common air temperature of about 24° was maintained. Plants were grown at these soil temperatures for 50 days and were then inoculated. The tomatoes grown at soil temperatures of 20° and 28° were large, vigorous, and succulent; those grown at either 12° or 36° were small, less succulent, and of low vigor (fig. 1, *A*).

After inoculation, the crocks were rearranged so that each temperature tank contained 2 crocks of plants predisposed at each soil temperature. Thus, for example, the 20° tank had 20 plants predisposed at 12°, 20 predisposed at 20°, 20 at 28°, and 20 at 36°. This set-up was duplicated for each host type, and disease development indices were recorded for each type of host predisposed at each soil temperature and under each postinoculation soil temperature condition. The disease development curves for Bonny Best and Marglobe plants grown at each predisposing soil temperature and held at 20° soil temperature after inoculation are shown in figure 2. Plants of both

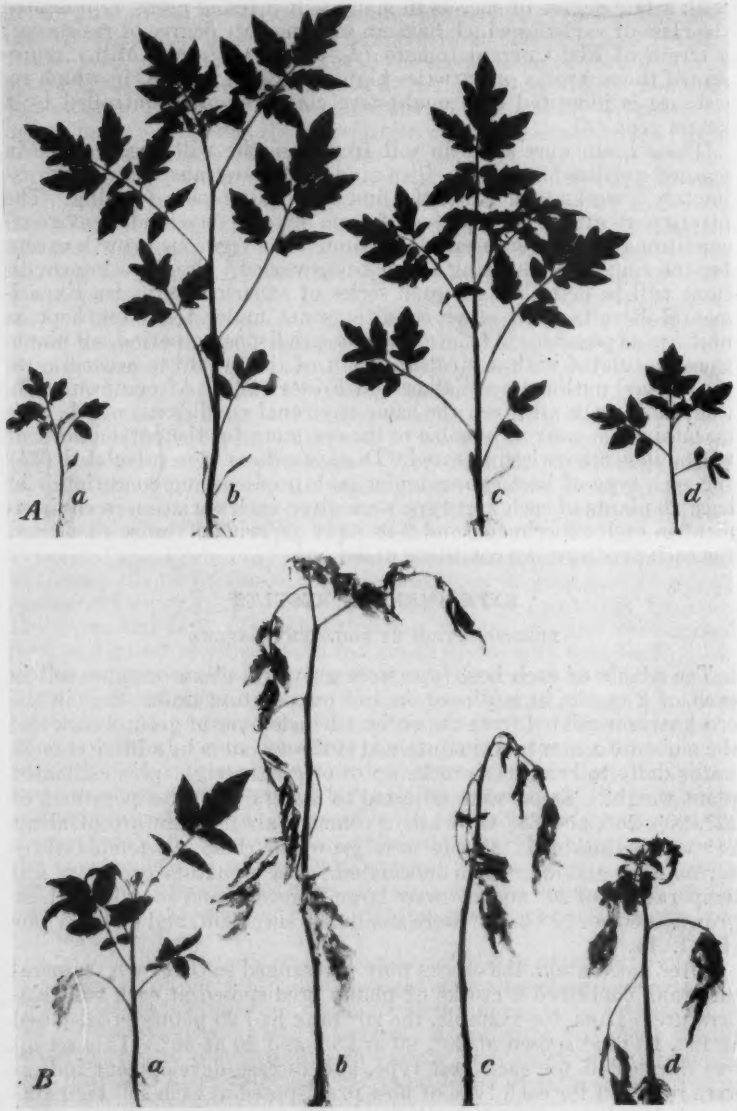

FIGURE 1.—*A*, Representative Bonny Best plants grown for 50 days before inoculation at the following soil temperatures: *a*, 12° C.; *b*, 20°; *c*, 28°; and *d*, 36°. *B*, Plants grown at the same temperatures and held at 20° soil temperature for 28 days after inoculation, with other environal conditions near optimum.

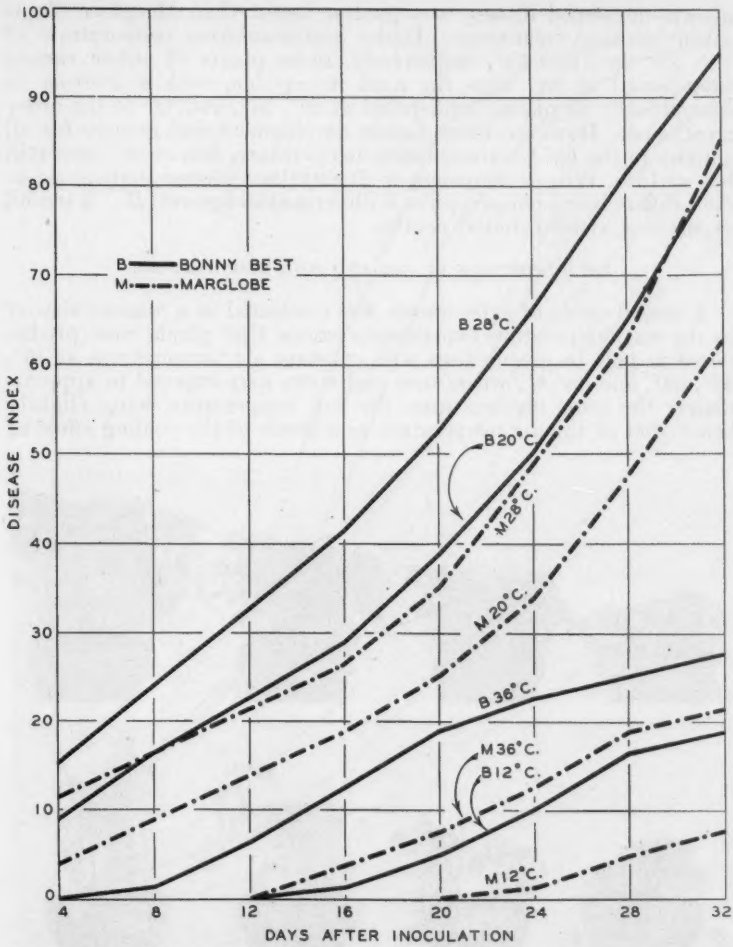

FIGURE 2.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 50 days at various soil temperatures (indicated for each curve), and held after inoculation at 20° soil temperature with all other environal conditions near optimum.

Bonny Best and Marglobe predisposed at 28° wilted most severely; those predisposed at 20° wilted less; those predisposed at 36° still less; and those predisposed at 12° wilted least. Bonny Best predisposed at 20° and Marglobe at 28° showed approximately the same degree of susceptibility. Red Currant retained its immunity under all conditions tested. The same relative susceptibility was manifested between varieties and between predisposing temperatures at all temperatures maintained after inoculation. Thus, Bonny Best plants

always developed disease to a greater extent than Marglobe plants given identical treatments. Under postinoculation temperatures of 12°, 20° 28°, and 36°, respectively, those plants of either variety predisposed at 28° were the most susceptible, with a decrease in susceptibility in plants predisposed at 20°, 36°, and 12° in the order mentioned. However, total disease development was greater for all entities in the 28° postinoculation temperature, less at 36°, and still less at 12°. Wilt development in Bonny Best plants predisposed at the 4 different soil temperatures is illustrated in figure 1, *B*. A second experiment yielded similar results.

PREDISPOSITION BY AIR AND SOIL TEMPERATURE

A second series of experiments was conducted in a manner similar to the soil temperature experiments except that plants were predisposed in pots in greenhouses with constant air temperatures at 16°, 20°, 24°, and 28° C., where tops and roots were exposed to approximately the same temperatures, the soil temperature being slightly below that of the air temperature as a result of the cooling effect of

FIGURE 3.—*A*, Bonny Best plants grown for 50 days before inoculation at the following soil and air temperatures: *a*, 16° C.; *b*, 20°; *c*, 24°; and *d*, 28°. *B*, Plants grown at the same temperatures and held at 24° soil and air temperature for 24 days after inoculation; all other conditions were near optimum.

evaporation. The largest, most vigorous, and most succulent plants were produced at 28° with a decrease in size, vigor, and succulence with each successive drop in predisposing temperature (fig. 3, *A*). After inoculation, plants predisposed at all of these temperatures were placed in each of the houses and wilt development was recorded for each unit. Disease index curves from a typical experiment with Bonny Best and Marglobe, predisposed at the four different temperatures and held at 28° after inoculation, are shown in figure 4. Plants

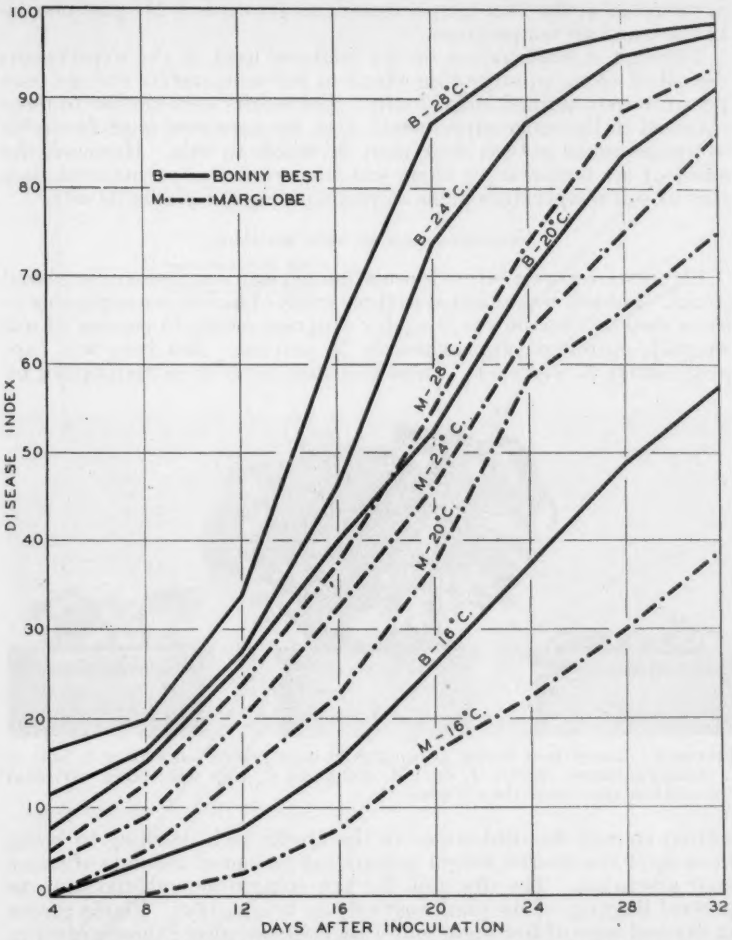

FIGURE 4.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 50 days at various soil and air temperatures (indicated for each curve), and held after inoculation at 28° soil and air temperature; all other conditions were near optimum.

predisposed at the same four air temperatures and given postinoculation temperature conditions of 24°, 20°, and 16° showed the same relative susceptibility. Total disease development during the term of the experiment, however, decreased as the postinoculation temperature was lowered. Tomatoes were most effectively predisposed to wilt at 28°, less so at 24° and 20°, and least at 16°. The disease reactions of Bonny Best predisposed at 20° and Marglobe at 28° were similar. Red Currant failed to develop wilt under any combination of conditions. Figure 3, *B*, shows wilt development in Bonny Best plants

predisposed at the four temperatures and grown at a 24° postinoculation soil and air temperature.

Through a combination of the methods used in the experiments described above, predisposing effects of soil temperature and air temperature were studied individually. The results were similar to those obtained in the other experiments, i. e., temperatures most favorable to tomato plant growth were most favorable to wilt. However, the effect of air temperature alone was somewhat less pronounced than that of soil temperature alone in predisposing the plants to wilt.

PREDISPOSITION BY SOIL MOISTURE

Plants were grown before inoculation in clean compost soil in glazed crocks. The soil was adjusted to three levels of moisture comparable to those used by Clayton (*4*), i. e., dry (approximately 15 percent of wet weight), optimum (approximately 30 percent), and very wet (approximately 37 percent). These moisture levels were maintained by

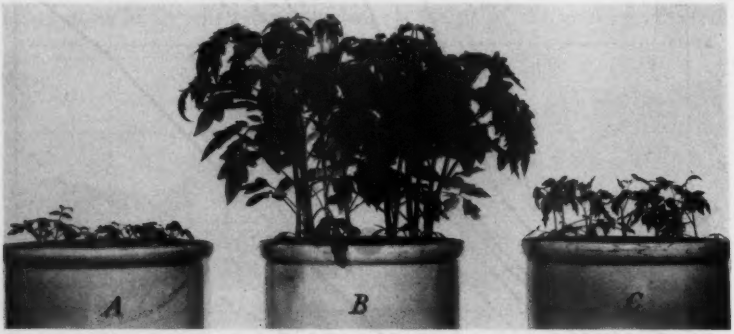

FIGURE 5.—Bonny Best plants grown for 30 days before inoculation in soil of various moisture levels: *A*, dry; *B*, optimum; *C*, very wet; other environal conditions were near the optimum.

adding enough distilled water to the crocks each morning to bring them up to the desired weight and adding measured amounts of water each afternoon. The dry soil did not contain enough moisture to prevent flagging of the plants entirely on bright days. Plants grown in dry soil were of low vigor and were least succulent; those grown in wet soil were also low in vigor, etiolated, and spindly. Soil of optimum moisture content produced normal, vigorous plants (fig. 5).

After being grown under the different soil moisture conditions for 30 days, plants were inoculated, transplanted into new soil in pots, and given optimum soil moisture as well as optimum soil temperature. Wilt development was recorded as before. Disease development curves from a typical experiment are shown in figure 6 for Bonny Best and Marglobe predisposed at the three soil moisture levels. With both the susceptible and the intermediate-resistant hosts, dry soil predisposed the plants to wilt, whereas very wet soil decreased potential susceptibility. No disease developed in Red Currant tomato.

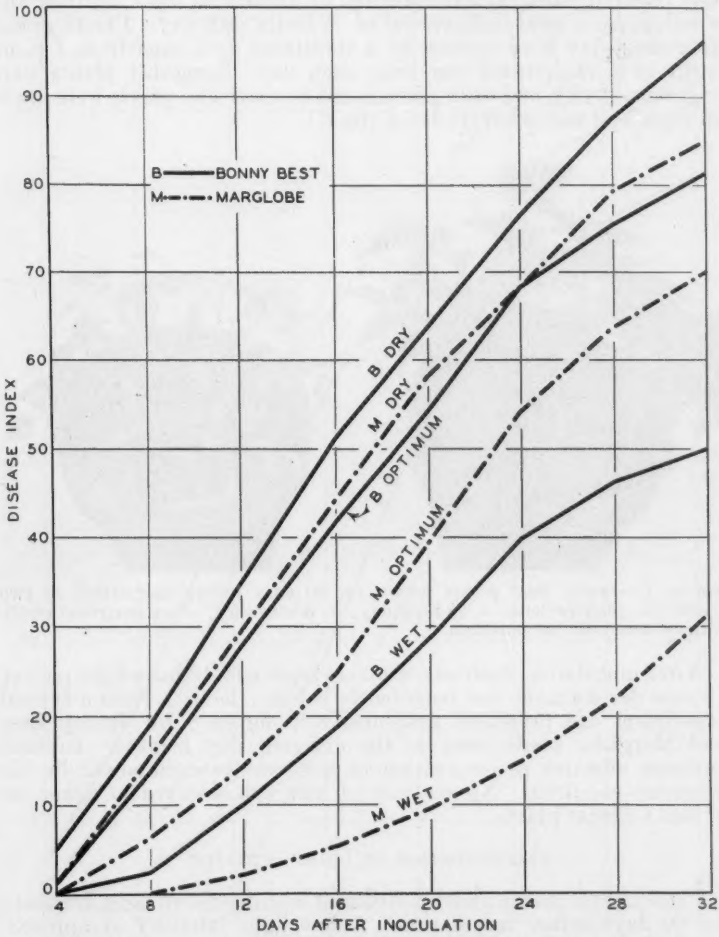

FIGURE 6.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 30 days in soil of various moisture levels (indicated for each curve) and held after inoculation in soil of optimum moisture content; other conditions were also optimum for wilt.

PREDISPOSITION BY LENGTH OF DAY

Eighty plants of each host type were grown for 30 days before inoculation in either a long or a short day. The plants grown in a long day received sunlight, supplemented by fluorescent light morning and evening, for a total light period of 18 hours each day. Plants grown in a short day were covered by a ventilated dark cage from 4 p. m. until 10 a. m., central war time, each day. Long-day plants were vigorous, stocky, and dark green in color; short-day plants were lower in vigor and somewhat etiolated (fig. 7).

FIGURE 7.—Bonny Best plants grown for 30 days before inoculation in two different photoperiods: *A*, 18-hour day; *B*, 6-hour day; other environal conditions were near the optimum.

After inoculation, both sets of plants received a 12-hour light period. Disease development was recorded as before; the data from a typical experiment are presented graphically in figure 8 for Bonny Best and Marglobe predisposed in the different day lengths. In both varieties effective predisposition to wilt was brought about by the short-day condition. No evidence of wilt was observed in either set of Red Currant plants.

PREDISPOSITION BY LIGHT INTENSITY

Plants were grown under 2 different conditions of light intensity for 30 days before inoculation. A low light intensity of approximately 90 foot-candles (range 60–110) was given 1 set of 80 plants of each host type by keeping them covered with a muslin cage. A comparable set received light of high intensity (approximately 800 foot candles, range 600-900) furnished by sunlight supplemented with artifical light from 200-watt Mazda bulbs. Plants grown in the light of greater intensity were normal and vigorous; those grown under reduced light were of low vigor and slightly etiolated (fig. 9).

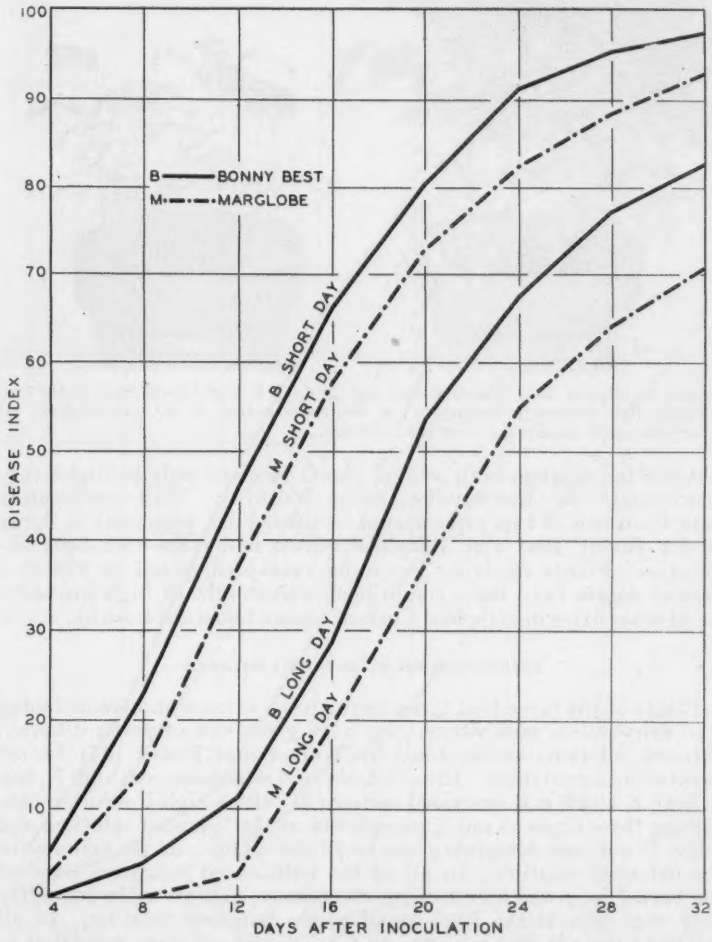

FIGURE 8.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 30 days in two different photoperiods (indicated for each curve), and given an intermediate-day length after inoculation; all other environal conditions were maintained near the optimum.

FIGURE 9.—Bonny Best plants grown for 30 days before inoculation under two different light intensity conditions: A, 800 foot-candles; B, 90 foot-candles; all other environal conditions were near optium.

After inoculation, both sets of plants received only sunlight (approximately 550 foot-candles, range 260–670). Wilt-development data from one of two experiments conducted are presented in figure 10 for Bonny Best and Marglobe grown under the two light intensities. Plants receiving less light were predisposed to wilt to a greater degree than those conditioned under light of high intensity. As in other experiments, Red Currant plants remained healthy.

PREDISPOSITION BY NUTRIENT BALANCE

Plants of the three host types were grown in sand and transplanted into drip-system pots where they were given one of seven different nutrient solutions as out lined by Walker and Foster (*24*) for 30 days before inoculation. The solutions used were balanced, high N, low N, high K and low K described earlier (*24*) and a high P solution containing three times as much phosphorus as the balanced solution, and a low P nutrient containing one-tenth the amount of phosphorus in the balanced solution. In all of the unbalanced solutions, none of the varied ions was ever lacking completely, and all other necessary ions were kept at the level found in the balanced solution. In all solutions the pH was adjusted to 6.5–7.0, and all were regulated to the same osmotic concentration by the addition of NaCl. In no case did the total $Na+$ or $Cl-$ ions approach an amount not readily tolerated by tomato plants.

Plants receiving the unbalanced solutions varied in size, but not in vigor or succulence, from those grown in the balanced solution. Plants grown in the high N, low N, high K and low K solutions were

somewhat smaller than the controls, while the plants grown before inoculation in the high or low P solutions were of the same approximate size as the controls. Excess or deficiency symptoms did not

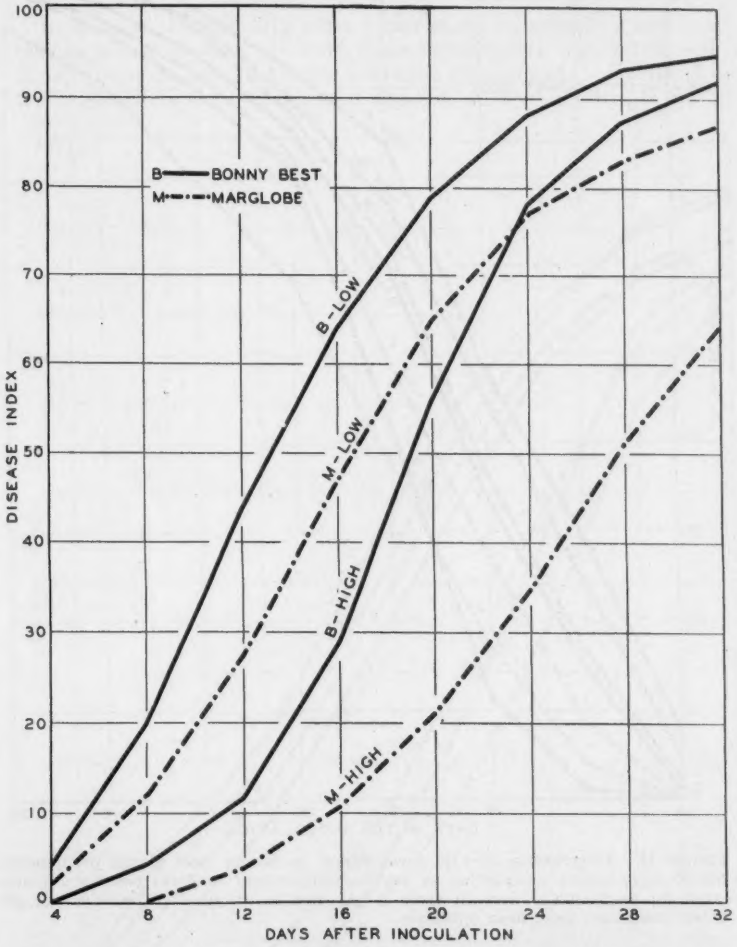

FIGURE 10.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 30 days under two different light intensities (indicated for each curve), and given an intermediate light intensity after inoculation all other environal conditions were near optimum.

develop in any of the plants. Following inoculation, the solution supply lines were cleaned thoroughly and the balanced solution was given to all plants. Disease development was recorded in the usual

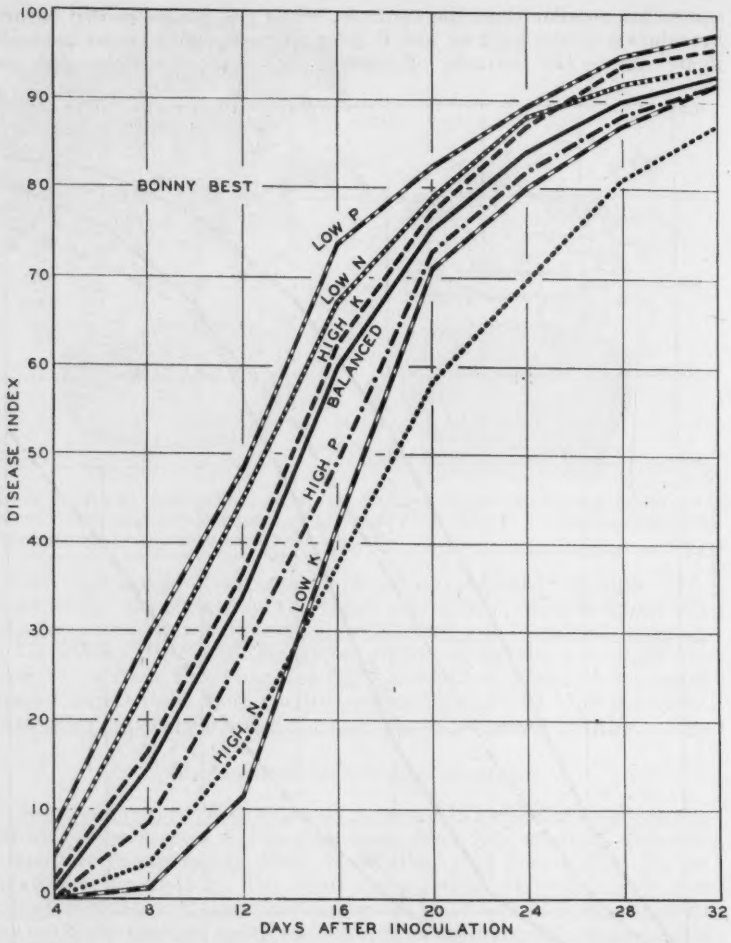

FIGURE 11.—Progression of wilt development in Bonny Best plants predisposed for 30 days before inoculation in various unbalanced nutrient solutions (indicated for each curve) and all given a balanced solution after inoculation; all other conditions were near optimum.

manner; data from a typical experiment are presented graphically for Bonny Best in figure 11 and for Marglobe in figure 12.

Predisposition most favorable to subsequent wilt development in both Bonny Best and Marglobe was brought about by low N, high K, and low P nutrition as compared with the balanced solution or with high N, low K, or high P, respectively. Decrease in potential susceptibility to wilt was found to have been conditioned in the plants by the solutions in the following order: Low P (most susceptible),

low N, high K, balanced solution, high P, low K, high N (least susceptible). Red Currant remained immune in all solutions.

PREDISPOSITION BY HYDROGEN-ION CONCENTRATION OF THE NUTRIENT

Because of the difficulty often experienced in adjusting and maintaining soil at a given pH level, these experiments were conducted in the drip-system along with the nutrition experiments. Balanced nutrient solutions were used, being adjusted in one case to pH 8.5 and

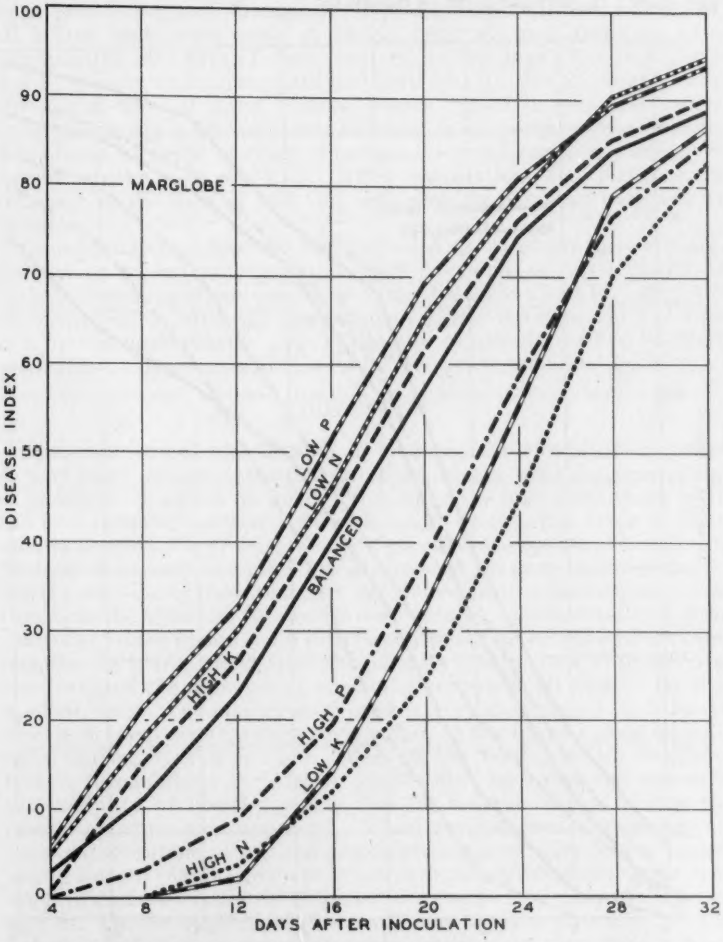

FIGURE 12.—Progression of wilt development in Marglobe plants predisposed for 30 days before inoculation in various unbalanced nutrient solutions (indicated for each curve) and all given a balanced solution after inoculation; all other conditions were near optimum.

in the other to pH 4.5. Plants grown in the balanced solution at pH 6.5–7.0 were used for comparison. Plants were grown for 30 days in these solutions before inoculation. Those grown in the high or low pH nutrients were slightly smaller than the plants grown in the balanced solution, but all were of normal color and succulence. Severe stunting and reduced vigor as described by Sherwood (*21*) for tomato plants grown in soil of high pH were not evident in the plants in this experiment. After inoculation, all plants received the balanced solution at pH 6.5–7.0. Wilt indices for Bonny Best and Marglobe are shown in graphic form in figure 13.

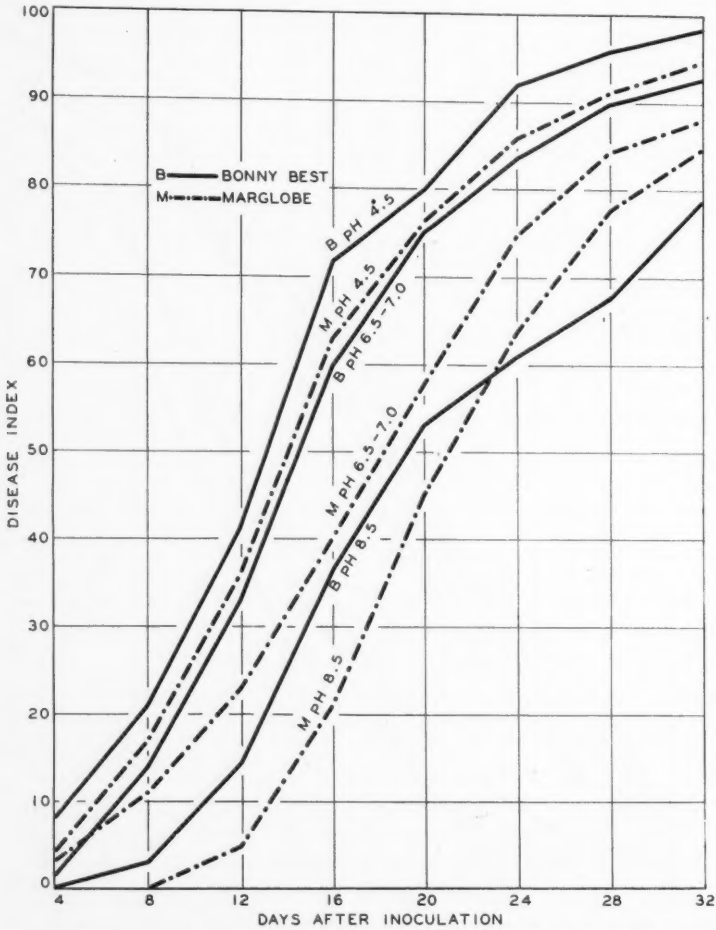

FIGURE 13.—Progression of wilt development in Bonny Best and Marglobe plants predisposed for 30 days before inoculation in balanced nutrient solutions of various hydrogen-ion concentrations (indicated for each curve), and given a solution of pH 6.5–7.0 after inoculation; all other conditions were near optimum

In both Bonny Best and Marglobe, plants grown in the low pH solution were more susceptible, while those grown in the high pH solution were less susceptible than those grown in the solution at pH 6.5–7.0. Neither predisposing condition had any effect on altering the complete resistance of Red Currant.

RELATION OF AGE OF HOST TO PREDISPOSITION

In order to study further the relation between size and vigor of the host and its predisposition to fusarium wilt, plants of different ages were inoculated, and disease development was recorded. Seeds of all 3 host types were sown at 10-day intervals and seedlings were transplanted into flats of clean compost soil 10 days after emergence and held under optimum conditions until 50-, 40-, 30-, 20-, and 10-day old plants were at hand. These plants varied in size and represented the range in size of plants obtained in all previous experiments. The plants, however, were all of normal color and succulence and were neither stocky nor etiolated. After inoculation, the plants were returned to the flats of soil and wilt development was recorded as before.

In neither Bonny Best nor Marglobe did age of plants have any significant or consistent effect upon wilt development. All plants of both varieties appeared to succumb to the disease at about the rate typical of the variety, although evaluation of disease development was difficult for the small plants. Age at the time of inoculation had no effect upon Red Currant since all plants of this strain remained healthy.

DISCUSSION

The complexities encountered in studying the effects of environal factors upon disease development emphasize the need for separating, if possible, the effects of such factors upon the host from those upon the host-parasite complex. An attempt to do this was made in these studies by subjecting healthy tomato plants to variations of one factor in the environment at a time, introducing the parasite, and then studying the reaction of these plants in an environment held, without variation, near the optimum for disease development. Differences in disease reaction of these plants could then be attributed to the effect of environment on the plants alone, since the parasite and the host after inoculation received the same set of environal factors at all times. By this method, most of the major environal factors were found to influence disease development through their action on the tomato plant as indicated earlier by Foster (*10*). Most of the factors which increased disease development in infected plants also increased the potential susceptibility of healthy plants, but for several of the factors, the reverse reaction was apparent. When soil temperatures alone, air temperatures alone, or soil and air temperatures combined, were varied, young tomato plants grown at levels near the optimum for growth of the host and for disease development were most favorably predisposed to wilt. On the other hand, the plants low in vigor grown in dry soil before infection were more favorably predisposed than the plants of high vigor grown in soil of optimum moisture content, while the plants of low vigor grown in very wet soil were the least favorably predisposed to the disease. The increase in susceptibility brought about in plants

grown in dry soil prior to infection is in contrast to the effects of soil moisture upon disease development after infection as reported by Clayton (*4*), who found wilt development to be retarded by both high and low soil moistures.

In the study of predisposition by day length and by light intensity, plants that received least light were found to be the most susceptible, a relation which is similar to that observed with infected plants growing in the greenhouse during winter months as contrasted with those growing during spring or summer months. Regarding these two factors, potential susceptibility of the hosts appeared to be correlated with low vigor. Under conditions of low light intensity or short light periods, the carbon-nitrogen ratio in the plants would be altered in favor of increased nitrogen. Therefore, the increase in susceptibility might have been brought about by the relatively higher nitrogen ratio in the plants. This indication regarding the relationship of the nitrogen ratio to potential susceptibility was not supported, however, by the results of experiments on predisposition by nutrient balance.

Walker and Foster (*24*) showed that infected tomato plants receiving unbalanced nutrients high in nitrogen or low in potassium developed wilt most severely as compared with infected plants grown in a balanced nutrient or in solutions low in nitrogen or high in potassium. In direct contrast, it has been shown in these studies that plants grown before inoculation in a solution low in nitrogen became more susceptible to wilt and those receiving nutrient high in nitrogen became less susceptible. The fact that high and low potassium solutions conditioned a comparable reversal in predisposing tomato plants suggests that these two elements are interdependent in some manner and may affect the potential susceptibility of the tomato to the wilt pathogen through their action upon a common factor. Shear and Wingard (*20*) pointed out that, according to several workers, deficiency of phosphorus resulted in an accumulation of nitrogen in tomato plants. Results of experiments conducted in this study are not in accord with this concept since the solution low in phosphorus brought about the same type of predisposition as did the low nitrogen nutrient, and also the high phosphorus and high nitrogen solutions had comparable effects on the potential susceptibility of the host. The effects of nitrogen and phosphorus were found to be similar in relation to disease development of cabbage yellows (*25*) but different in cabbage clubroot (*26*). In the studies on predisposing tomato plants by unbalanced nutrition, no correlation between host size or vigor and susceptibility was apparent.

In sand culture, tomatoes grown in a solution of high pH were less susceptible to wilt; those grown in a low pH nutrient were more susceptible. While the relationship of susceptibility to pH may be different in plants grown in soil, these findings are in accord with those of Edgerton and Moreland (*9*), who reported a decreased wilt development in tomatoes grown on limed soil. Also Sherwood (*21*) presented evidence that wilt was most severe in tomato plants grown on acid soils. Again, the somewhat smaller and less vigorous plants grown in solutions of either high or low pH were more or less susceptible depending upon the treatment they had received before inoculation.

That the size and vigor of tomato plants are not consistently correlated with susceptibility to wilt is shown by the preceding experiments. This was substantiated still further in the experiments on age of plants in relation to predisposition. Plants varying in age and thus in size all showed approximately the same potential susceptibility, which leads to the conclusion that predisposition to wilt may be induced in tomato plants by a number of major factors in the environment and that variation in those factors may or may not affect the size and vegetative vigor of the plants.

Susceptible Bonny Best and intermediate resistant Marglobe were predisposed in very nearly the same manner by variations in the environment. Under a certain set of environal conditions, Marglobe may be made to appear as susceptible as Bonny Best grown under another set of conditions. Similarly, by controlling the environment in which it is grown, Bonny Best may be reduced in potential susceptibility to the level normally shown by Marglobe. From this it is apparent that the type of resistance carried by Marglobe is variable, and a similarity to type B resistance of cabbage to yellows (*1*, *25*) is suggested. Since Red Currant plants showed no evidence of the disease under any of the conditions tested, it is to be concluded that these plants carry a type of resistance closely approaching true immunity and that this high degree of resistance may be attributed to a character or characters little influenced in their expression by the environment.

In tomato plants inherently susceptible or partially resistant to *Fusarium oxysporum* f. *lycopersici*, a wide range of disease reaction has been obtained by varying the environment acting upon the host previous to inoculation and not upon the pathogen or the host-pathogen complex. This leads to the conclusion that the relation of environment to disease development in many cases may be attributed, in part at least, to the effect of environment in the host alone, while in other cases, factors in the environment apparently assert their over-all effects largely upon the host-pathogen complex, overcoming changes in potential susceptibility or resistance conditioned in the host prior to infection. The nature of predisposition occasioned by temperature, light, and high water content, and pH of the substrate are examples of the former possibility; low soil water and unbalanced nutrition exemplify the latter.

It is recognized that, in the greenhouse experiments conducted in this study, certain extremes in conditions were used to facilitate recognition of the effects of environal factors. Methods of growing and inoculating plants were often such as are infrequently encountered in the field. While direct comparisons cannot be made in all cases with field-grown plants, tendencies or trends in altered potential susceptibility occasioned by certain environal factors have been clearly demonstrated and the phenomenon of predisposition has been shown to be of major importance in the consideration of environment in relation to wilt development.

SUMMARY

By subjecting healthy young tomato plants to variations in the environment only before inoculation and then maintaining a constant

and optimum set of conditions for wilt development after inoculation, the effect of environal factors on disease development through action upon the host alone was studied. Tomatoes were found to be favorably predisposed to wilt (*Fusarium oxysporum* f. *lycopersici* (Sacc.) S. & H.) by the following entities of the environment: (1) Soil or air temperature near the optimum for plant growth, (2) low soil moisture, (3) short day length, (4) low light intensity, (5) nutrient low in nitrogen, low in phosphorus, or high in potassium, and (6) nutrient low in pH. Potential susceptibility of the plants was found to be decreased and consequently their resistance increased by soil or air temperatures above or below the optimum for plant growth, by very wet soil, by long daylight periods, and by high light intensity. Decreased susceptibility was also conditioned in plants grown in solutions high in phosphorus, low in potassium, or high in nitrogen and also in solutions with a high pH.

Neither size nor vigor of the host as determined by particular variations in environal conditions or by age of the plants at the time of inoculation showed any consistent correlation with subsequent wilt development.

Susceptible Bonny Best and intermediate-resistant Marglobe were both predisposed to wilt by the same environal factors and apparently in the same manner. Resistant plants were made to appear susceptible, or normally susceptible hosts were conditioned so as to appear resistant, by proper control over the environment in which they were grown prior to infection. It was not possible to alter the high degree of resistance found in the strain of Red Currant tomato used.

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EFFECT OF INDOLE-3-BUTYRIC ACID ON TRANSPLANTED PECAN TREES [1]

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INTRODUCTION

Recently indole-3-butyric acid was applied to roots of nursery-grown trees of pecan (*Carya illinoensis* (Wang.) K. Koch) at the time of transplanting to stimulate root formation. During the experimentation [2] it was found that when 8 mg. of the acid per tree was applied to the taproots the trees averaged 39 percent more new shoot and leaf growth than did similar trees treated with 16 mg. of the acid, but it was not clear whether the larger amounts of indole-3-butyric acid inhibited new top growth directly or stimulated new root formation and growth and thus indirectly inhibited top growth by utilizing greater amounts of the stored nutrient materials. Marth [3] found that certain growth-regulating chemicals applied to the whole plant effectively inhibited growth of buds on rose bushes during 40 to 60 days in common storage and that the starch content of the treated bushes was conserved during storage; as a result the treated bushes made more root and shoot growth when transplanted to the field than did similar untreated ones.

In order to determine the effects of indole-3-butyric acid on the composition of the tissues of transplanted pecan trees, experiments were conducted during the 1944 growing season at Brownwood, Tex.

MATERIALS AND METHODS

Seedling pecan trees 4 to 6 years old were selected and divided into seven uniform lots. Each lot contained six 6-year-old trees and eight 4-year-old ones; the trees were selected for uniformity of size and for type of root system and top. They were dug on April 5 and 6 and carefully heeled in. On April 7 the taproots of three lots were treated with indole-3-butyric acid, and they and three similar untreated lots were then transplanted to the field. The treatments consisted of boring small holes at four different places in the taproot of each tree and

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[2] SMITH, C. L., and ROMBERG, L. D. THE USE OF INDOLEBUTYRIC ACID AS AN AID IN TRANSPLANTING PECAN TREES. Tex. Pecan Growers Assoc. Proc. 21: 17–22. 1941.

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inserting in each one-half of a round toothpick containing approximately 2 mg. of indole-3-butyric acid. Thus, 8 mg. of the chemical was inserted in the taproot of each treated tree. The toothpicks were prepared by soaking in an alcoholic solution of the acid and then allowing the alcohol to evaporate.[4]

One lot was sampled for analysis at the beginning of the experiment, on April 7. One lot each of treated and untreated trees was dug and sampled for analysis on June 28, on September 5, and on October 12, in order to follow the progressive changes in composition during the growing season. The new roots, shoots, and leaves were removed at the time of digging, and the dry weights were determined. Samples of trunks, including wood and bark, were taken by sawing through the trunk of each tree in the lot, collecting the sawdust, and compositing it for sampling. Those of taproot wood were taken similarly after the bark had been stripped from a 12-inch section at the middle of each. The taproot bark from all the sections was chopped fine with shears and after thorough mixing was sampled for analysis.

Analyses were made of dry matter, reducing and nonreducing sugars, starch, hemicellulose,[5] and organic nitrogen. The methods of preserving the samples and of analyses were the same as those used by Thor and Smith[6] except as stated. Organic nitrogen was determined by the official Kjedahl-Gunning-Arnold method,[7] and the cuprous oxide in the analyses of sugars, starch, and hemicellulose was determined by direct weighing. Dry matter was calculated as a percentage of fresh weight, and all other elements were calculated as percentages of dry matter.

EFFECT OF TREATMENT ON COMPOSITION

DRY MATTER

The percentages of dry matter in the trunks of treated and untreated trees were approximately the same except on June 28 (fig. 1, *A*). On that date the percentage had increased considerably in untreated trees, while in the treated ones there was a corresponding decrease. Although the percentages in the wood of the taproots decreased generally throughout the season, the decrease was greater in treated trees than in untreated ones. The percentages were always higher in the bark of taproots of untreated trees than in that of treated ones, although the fluctuations were in different directions on June 28 and September 5.

REDUCING SUGARS

The percentages of reducing sugars were low and fluctuated similarly in the trunks of treated and untreated trees (fig. 1, *B*). Those in the taproot wood increased in both cases, but on all sampling dates the percentages for the treated trees were about three times those for

[4] See footnote 2, p. 187.

[5] Hemicellulose as used here includes the carbohydrate bodies hydrolyzed by dilute mineral acids but not by diastase.

[6] Thor, C. J. B., and Smith, C. L. A physiological study of seasonal changes in the composition of the pecan during fruit development. Jour. Agr. Res. 50: 97–121, illus 1935.

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the untreated ones. Although the percentages were higher in the taproot bark of untreated trees than in that of the treated ones, the fluctuations were similar.

NONREDUCING SUGARS

The curves for the nonreducing sugars in the trunks and taproot bark of treated trees differed little from the corresponding curves for untreated ones (fig. 1, *C*). The percentages in the taproot wood of the

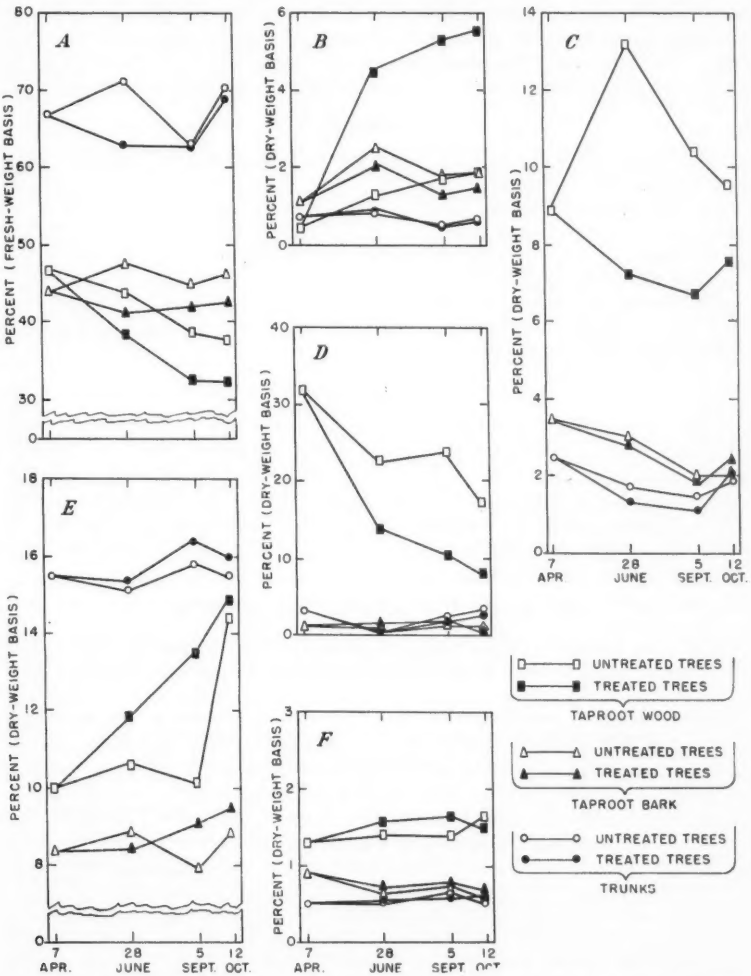


FIGURE 1.—Seasonal changes in dry matter (*A*), reducing sugars (*B*), nonreducing sugars (*C*), starch (*D*), hemicellulose (*E*), and organic nitrogen (*F*) in untreated (normal) pecan trees and in similar ones whose taproots received an application of 8 mg. of indole-3-butyric acid prior to transplanting, 1944.

treated seedlings, however, were much smaller than those in that of the untreated, which showed a sharp increase from April 7 to June 28 and a similar decrease to October 12. The increase on June 28 was in sharp contrast to the decrease in treated trees. At the end of the experiment the taproot wood of untreated trees contained more nonreducing sugars than did that of the treated trees.

STARCH

The treatment apparently had little effect on the low percentages of starch in the trunks and taproot bark (fig. 1, *D*). On the contrary, it caused a considerable reduction in the high starch content of the taproot wood; during the season the percentages decreased from 31.89 to 8.15 and 17.30, respectively, in the treated and the untreated trees.

HEMICELLULOSE

The percentages of hemicellulose in the trunks were not appreciably affected by the treatment (fig. 1, *E*). In the taproot wood of treated trees the percentage increased rapidly throughout the experiment in contrast to that in untreated trees, which fluctuated slightly from April 7 to September 5, and then increased very sharply to October 12, when it was almost as high as that in treated trees. Although the percentages fluctuated somewhat differently in the taproot bark of treated and untreated trees, it is doubtful whether the hemicellulose content was affected by the treatment.

ORGANIC NITROGEN

The curves for percentages of organic nitrogen in the trunks and taproot bark of treated and untreated trees differed little and fluctuated similarly (fig. 1, *F*). In the taproot wood of treated trees the percentages increased appreciably from April 7 to September 5, but they remained almost constant in that of untreated trees. Because of opposite trends during the last period of the experiment the final percentages were about equal.

EFFECT OF TREATMENT ON GROWTH

At each sampling date the new root and shoot growth was much greater in treated trees than in similar untreated ones (table 1). The

TABLE 1.—*Effect of indole-3-butyric acid treatment of taproots on the growth of transplanted, nursery-grown, 4- to 6-year-old pecan trees, 1944*

[Treatment, 8 mg. per taproot; each value based on 14 trees]

Sampling date and status of trees	Average dry weight per tree of—	
	New roots	New shoots and leaves
	Grams	*Grams*
June 28:		
Treated	2.07	6.54
Untreated	.04	3.91
September 5:		
Treated	4.92	12.74
Untreated	.55	8.43
October 12:		
Treated	4.20	24.10
Untreated	.54	12.07

ratio of new root growth of treated to that of untreated trees was, however, much greater than the similar ratio for growth of new shoots and leaves. This indicates that indole-3-butyric acid stimulates the initiation and growth of roots to a greater extent than it does shoots and leaves.

INTERRELATION OF CHANGES IN COMPOSITION

In a comparison of the changes in percentage composition of the different tissues of treated and untreated pecan trees during the 1944 season, it was found that in the majority of casee where changes occurred they were in the same direction but not to the same extent. The main exception was in the percentage of nonreducing sugars of taproot wood, where the changes in treated trees were in the reverse direction from those in untreated ones. As a general rule greater changes occurred in the percentage composition of tissues of treated trees than in those of untreated; the former also made more new root and top growth, and therefore greater changes in composition were to be expected.

In both treated and untreated trees most of the elaborated food materials available for growth functions during the experiment were those stored at the time of transplanting, because the trees had small root spreads for absorption of soil nutrients and produced few leaves for photosynthetic processes, particularly during the first part of the experiment. Thus, it is not surprising that the main changes in percentage composition in the tissues analyzed were centered around those in starch content, especially in the taproot wood. The highest starch content was found in taproot wood; the greatest changes in percentage composition and the greatest difference between the changes in treated and untreated trees occurred in this tissue. The starch content of taproot wood was high at the beginning of the experiment and the percentages decreased greatly during the season, but the decrease was about 1.6 times as great in treated trees as in those not treated.

The percentage of dry matter in taproot wood of treated trees also decreased to a much greater extent than did that in untreated ones. The percentages of reducing sugars were much higher in taproot wood of treated trees than in that of untreated ones, but the reverse was true of nonreducing sugars; consequently, the differences in percentages of total sugars in taproot wood of treated and untreated trees were not great.

The percentage of hemicellulose in taproot wood of treated trees increased rapidly throughout the experiment, whereas in that of untreated ones the changes were relatively small until the final stage of the experiment, when the percentage increased sharply. The increases in percentages of hemicellulose in taproot wood, as well as the variations in percentages of the other constituents, may be largely accounted for by the decreases in the percentages of starch. The starch percentages decreased very rapidly, indicating an actual decrease in starch content. Since starch made up almost one-third of the dry matter of taproot wood at the beginning of the experiment, a rapid decrease in its percentage (dry-weight basis) would mean a corresponding decrease in percentage of dry matter; this is what occurred. Therefore, if there were little or no change in the actual amount of hemicellulose

in taproot wood during the experiment, the percentages (dry-weight basis) would increase in proportion to the decrease in starch or other dry matter; in fact, the actual amounts of hemicellulose could decrease under such conditions while the percentages increased for the same reason.

It is likely that there were actual decreases in nonreducing sugars in all of the analyzed tissues of treated trees, since the percentages on the dry-weight basis decreased during the experiment.

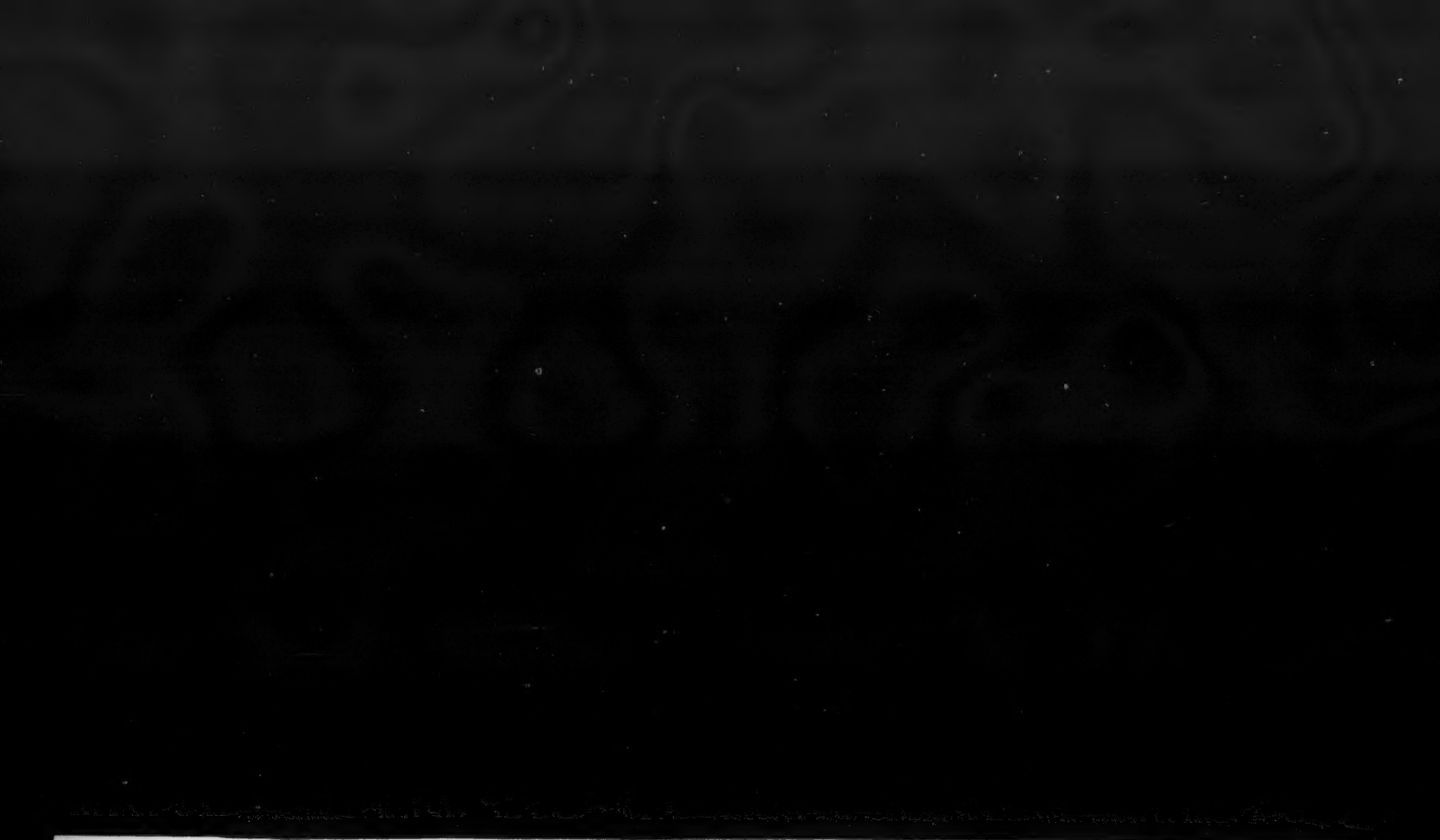
SUMMARY AND CONCLUSION

The taproots of nursery-grown pecan seedlings were treated with approximately 8 mg. of indole-3-butyric acid per tree at the time of transplanting, and the percentages of sugars, starch, hemicellulose, organic nitrogen, and dry matter of the taproot wood, the taproot bark, and the trunks at intervals during the first growing season were compared with those for the tissues of similar untreated trees.

As a whole, the important changes in composition of the trees may be centered around the decreases in starch content, particularly in the taproot wood, in which the percentage of starch was very high (31.89 percent of dry matter) at the beginning of the experiment and the decrease during the season was 1.6 times as great in treated trees as in untreated ones. The decreases in starch content would affect the percentages of other materials such as sugars and hemicellulose (dry-weight basis) and dry matter (fresh-weight basis) in proportion to the decreases in starch. Considerable changes occurred in percentages of nonreducing sugars, but it would appear that changes in the labile forms of carbohydrates are of less value in a study of the effects of the indole-3-butyric acid than are changes in amounts of starch from which they probably were derived, since the equilibrium levels of the labile forms may fluctuate more than those of starch.

There were changes in the composition of the trunks and the taproot bark, but they were largely in the same direction in treated and untreated trees, and the differences can probably be explained on the same basis as the changes in composition of taproot wood.

The treated trees made more new root and shoot growth than untreated ones; as would be expected there were greater changes in the chemical composition since the trees were largely dependent on stored nutrient materials to support growth functions during the period of the experiment.

It is therefore apparent that a relatively small quantity of indole-3-butyric acid, when applied to taproots of transplanted pecan trees, stimulates the processes of initiation and growth of new roots and of top growth; as a consequence greater amounts of the stored nutrient materials are used up during the first growing season than in similar untreated trees.

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